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AN ASSESSMENT OF SOME INTERNAL CHARACTERS IN THE HIGHER CLASSIFICATION OF THE CURCULIONIDAE *S.L.* (COLEOPTERA)

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[Communicated by Mr. R. G. Davies]

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With 186 Text-figures

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I. Introduction and Review of Literature

Though they form a very large and variable group, with many economically important species, the Curculionidae *s.l.* have never been systematically investigated by the comparative morphologists. Their higher classification has been attempted largely on the basis of external characters of adults and larvae such as normally attract the attention of taxonomists, and it remains a field in which a large number of unresolved difficulties persist. The various authorities disagree on the limits of the higher groups and on the phylogenetic relationship of the various subfamilies and tribes which have been recognised ; to quote Crowson (1955), the subject constitutes " the largest and the most important outstanding problem in the higher classification of the Coleoptera ". The present work does not, of course, claim to provide a definite solution of these problems, nor is it suggested that a satisfactory classification can be created from the study of internal characters alone. An adequate appraisal of the taxonomy and phylogenetic relationships of weevils must await a far fuller knowledge of internal and external characters throughout the group (as well as data provided by the larvae and by non-morphological information). The following historical survey is therefore provided in order to demonstrate that the scarcity of existing information on internal anatomy justifies the work undertaken here on this subject.

Nüsslin (1911–12) made one of the most important contributions in a study of the bark beetles (Scolytinae and Ipinae). He constructed keys to the genera, based on the male and female reproductive organs and proventriculus, and discussed the

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mid gut and Malpighian tubules. He revealed the taxonomic importance of many of these structures, but did not describe the various species individually. In many ways the present work may be regarded as an extension of Nüsslin's approach.

Chararas (1956) gave an account of the comparative anatomy and biology of larvae and adults of ten species belonging to nine genera of Cossoninae and Scolytinae. He compared them on the basis of a few characters of the proventriculus, mid gut, Malpighian tubules and reproductive organs, drawing attention to the great diversity of the testes and male accessory glands as contrasted with the relative uniformity of the female reproductive system. He also showed that some cossonines have only four Malpighian tubules.

Other work on the internal anatomy of the Curculionidae has mostly been carried out as part of a comparative survey of single organ-systems in the Coleoptera generally. For example, Poll (1932) has dealt with the Malpighian tubules and developed a phylogenetic grouping in which Chrysomelidae, Bruchidae, and Curculionidae (including Scolytidae) have " six Malpighian tubules with their true insertions grouped in four and two, the arrangement of the false insertions not being constant ". Further, Stammer (1934) gave an account of the Malpighian tubules in the Coleoptera and showed quite a few arrangements of anterior and posterior insertions within the weevils. He recognised six as the primitive number; apionids have four or six tubules, two of the latter being modified into symbiont-carrying structures. Again, Heberdey (1931), in an account of the female reproductive system of beetles, recognised two types of accessory glands in the Coleoptera: the first type (in Cleonini and Lixini) open between the eighth and ninth abdominal sternites, while the second type (numerous curculionids, including Ipinae) open into the vagina. Buchner (1953) has summarised his and other researches on the symbiont-containing organs of weevils. He reports that on each side of the female reproductive tract there is a single club-shaped organ in *Cleonus piger* (Scop.) a long tubular one in *Lixus nitidicollis* Fbr., and a bundle of tubular ones in *Larinus sturnus* Schall.; he also mentions the presence of symbiotic bacteria in the two short Malpighian tubules of apionids, in mycetomes around the gut in *Rhynchophorus ferrugineus* Ol. and in the terminal chambers of the ovaries of some Ipinae. Works by Scheinert (1933) on Cleoninae, Nolte (1937) on *Apion*, and Pierantoni (1927), Mansour (1930) and Tarsia-in-Curia (1933) on *Calandra* may also be mentioned here. Finally, the central nervous system has received a little attention (*e.g.* Brandt, 1879; Dönges, 1954) and Imms (1957) mentions that two abdominal ganglia occur in Curculionidae. Tanner (1943) has used the spermatheca in the subtribe Hydronomi at generic as well as specific levels. Otherwise, published work on the internal anatomy of the Curculionids consists of accounts of one or more systems in a single species. These are too numerous to discuss here, but are mentioned and incorporated in the descriptive section below.

Enough has been said to indicate that the few data available suggest that many useful taxonomic and phylogenetic conclusions might emerge from a more extensive survey of the internal anatomy of the Curculionidae. This feeling is strengthened when one notes the way in which a detailed knowledge of the internal anatomy of other groups has contributed significantly to their taxonomy. Hinton was one of the first to emphasize this in the Coleoptera, as his work on Dryopoid beetles and *Gyrelmis* shows (Hinton, 1939, 1940). Other comparative work, though less detailed or confined to the importance of one or two internal organs, may be found in several groups. For examples, Spett and Lewitt (1928) and Varma (1955) drew attention to the value of the spermatheca at higher and lower levels of the classification of the Chrysomelidae, Ehara (1952, 1953) used the spermatheca at the specific level in the same family, and Donia (1958) indicated the taxonomic value of various features of the reproductive systems in a study of 19 species of Chrysomelidae. Finally, one may mention that in the Heteroptera, studies of the reproductive system (Pendergrast,

1957) and salivary glands (Baptist, 1941; Southwood, 1955) have contributed greatly to modern views on the higher classification of the suborder.

II. Material and Techniques

The species studied have been listed in the order of subfamilies and tribes given by Winkler (1924–32), but I have used modern names with Winkler's equivalents in brackets.

Rhynchitinae

Deporaus betulae (L.)

Apioninae

Apion miniatum Germ.
A. ulicis (Forst.)
A. frumentarium (Payk.)
A. radiolus Kirby
A. immune Kirby

Otiorrhynchinae

Otiorrhynchus singularis (L.)
Myllocerus sp. nov.
M. maculosus Desb.
Phyllobius pyri (L.)
P. virideaeris (Laich.)

Brachyderinae (+ Tanymecinae)

Polydrosus tereticollis (DeGeer)
Strophosomus melanogrammus (Forst.)
Parisomias sp. nov.

Eremninae

Amblyrrhinus subrecticollis Marsh.
Amblyrrhinus sp. nov.

Sitoninae (Brachyderinae *part*)

Sitona regensteinensis (Hbst.)
Sitona sp.

Cleoninae

Hypolixus truncatulus Fab.
Conorhynchus brevirostris Gyll.
Xanthochelus faunus Ol.
Neocleonus sanio Hbst.

Cossoninae

Pentarthrum huttoni Woll.

Bagoinae

Bagous sp.

Erirrhininae (Notarinae)

Dorytomus tortrix (L.)
D. rufatus (Bed.)
D. dejeani (Fst.)

Tychiinae (Tychiini)

Miccotrogus picirostris (Fab.)
Sibinia arenariae Steph.

Anthonominae (Anthonomini)

Anthonomus pedicularius (L.)
A. inversus Bed.

Balaninae (Curculioninae)

Balaninus venosus (Grav.)
Balaninus glandium (Marsh.)
Balanobius pyrrhoceras Marsh.
Balanobius salicivorus (Payk.)

Hylobiinae

Hylobius abietis (L.)

Hyperinae (Hyperini)

Hypera punctata (Fab.)
Hypera murina (Fab.)

Rhytirrhininae

Gronops lunatus (Fab.)

Rhynchophorinae

Sitophilus oryzae (L.)
Cosmopolites sordidus Aur.
Rhynchophorus sp.

Ceuthorrhynchinae

Coeliodes rubicundus (Hbst.)
Micrelus ericae (Gyll.)
Cidnorrhinus quadrimaculatus (L.)
Ceuthorrhynchus pollinarius Forst.
Rhinoncus pericarpius (L.)

GYMNETRINAE (MECININAE)

Gymnetron pascuorum (Gyll.)
Gymnetron antirrhini (Payk.)

ALCIDODINAE (MECININAE *part*)

Alcidodes fabricii Fab.

CIONINAE (MECININAE *part*)

Cionus scrophulariae (L.)
Cionus sp.

ANOPLINAE

Anoplus plantaris (Naez.)

RHYNCHAENINAE

Rhynchaenus fagi (L.)
R. rusci (Hbst.)
Rhamphus pulicarius (Hbst.)

SCOLYTINAE

Scolytus destructor Ol.

HYLASTINAE (IPINAE)

Hylastinus obscurus (Marsh.)
Myelophilus piniperda (L.)
Phloeophthorus rhododactylus (Marsh.)

The internal systems were studied from the freshly dissected insects. Bouin's fluid was used to fix the different systems for drawing. The central nervous system was studied in weevils fixed in Bouin's fluid. The spermathecae and proventriculus were dehydrated, stained in acid fuchsin or borax carmine, cleared and mounted in balsam. A squared eyepiece was used in drawing the alimentary canal and reproductive systems. The sketches of the central nervous system, spermatheca and proventriculus were made with the help of a camera lucida.

In regard to the terms applied in the text: (i) Nüsslin (1911) has been followed in describing the proventriculus; (ii) in the spermatheca, the terms collum and ramus of Spett and Lewitt (1928) have been used; (iii) vagina includes, in some species, the long sclerotised part called " ovipositor " by some authors.

III. THE ALIMENTARY CANAL

The alimentary canal comprises the usual three parts, *i.e.* fore, mid and hind gut. The narrow pharynx opens into the tubular oesophagus, which is narrow anteriorly but may be distended posteriorly to form a crop (absent in a number of weevils). The proventriculus is either absent, poorly defined or weakly or strongly developed. When the grinding plates are present, each may be paired or unpaired according to whether the median is continued or fused anteriorly. The blade is well defined, rounded and truncate or notched anteriorly in those species without the grinding plates. The retaining bristles vary in length and may be absent altogether. The declivity teeth may be present or absent. The development of the brushes of the blade is also variable. The median may be marked throughout the length of the blade, thus giving the latter a paired appearance. The adjacent grinding structures may be incised or straight anteriorly at the intermedians. The external intermedial fringe is normally present and varies in length. This fringe has not been mentioned by previous authors. In some species the crop or, where this is absent, the posterior part of the oesophagus is clothed internally with bristles which are arranged in rows or scattered over the whole surface, though they are seldom present in the cardiac valve.

The mid gut is divided into two parts; the anterior part is distended and the posterior one tubular. The distended part is ovoid, tubular or broad in front and narrows posteriorly. Its walls are smooth or wrinkled, with or without enteric caeca and symbiont-containing structures (Buchner, 1933, 1953). Enteric caeca are also present at the front of the mid gut in the cossonids, and all over in Rhynchophorinae; other weevils lack these caeca. The tubular part of the mid gut is sometimes of uniform diameter, sometimes not, and it generally loops under the anterior part. It bears from one to numerous enteric caeca, which vary in arrangement and position.

The hind gut is a convoluted tube of variable diameter. Towards its posterior end it bends sharply back on itself (the posterior flexure). It is at or near this flexure that the distal ends of the Malpighian tubules are applied to the gut wall. Behind the posterior flexure the gut broadens gradually and is usually sharply constricted, then continued as a tube of uniform diameter to the anus. Sometimes the constriction is not well defined and this part is irregularly distended.

Four or six Malpighian tubules are present and are all normally cryptonephridial. They arise from the posterior end of the mid gut. In the hexanephridial type, two of the tubules may be modified into the club-shaped structures mentioned as carrying the symbiotic bacteria by Stammer (1934), Buchner (1953) and others. In other hexanephridial species, two tubules out of six are sometimes shorter and narrower than the others. The tubules vary in arrangement with respect to the mid and hind gut and are described under each species.

Deporaus betulae (L.) (fig. 1)

Crop and proventriculus absent.

Midgut with distended part smooth, ovoidal, without enteric caeca or symbiont-containing structures ; tubular part coiled, with two rows each of 8–14 enteric caeca on posterior half ending a little distance before the insertion of Malpighian tubules.

Hind gut shorter and narrower than the mid gut, gradually broadened behind posterior flexure and then abruptly contracted into a tube of uniform diameter.

Six long Malpighian tubules inserted in two groups, three tubules in each group ; applied separately just behind posterior flexure.

Rozsypal (1939) has shown a well developed crop, two rows of enteric caeca and six tubules inserted all round the gut anteriorly in *Rhynchites pauxillus* Germ.

Apion miniatum Germ. (fig. 2)

Oesophagus slightly broadened posteriorly ; crop and proventriculus absent.

Mid gut with distended part indented anteriorly at junction with oesophagus, smooth, broadest at about middle, narrowed at both ends and without enteric caeca or symbiont-containing structures ; tubular part with anterior half of uniform diameter, then narrowed and with two rows each of 8–14 enteric caeca posteriorly.

Hind gut about as broad at junction as the mid gut, and as long, narrowing to the application of Malpighian tubules ; behind this again broadened and then contracted into a broad tube ; posterior flexure not distinct.

Six Malpighian tubules inserted anteriorly in two groups, one of four long tubules and the other of two short ones modified into stalked and dumb-bell-like structures ; the four long tubules applied to the mid gut posteriorly in two groups of two, one group on each side, the two short tubules (which carry symbionts) not applied.

Apion frumentarium (Payk.)

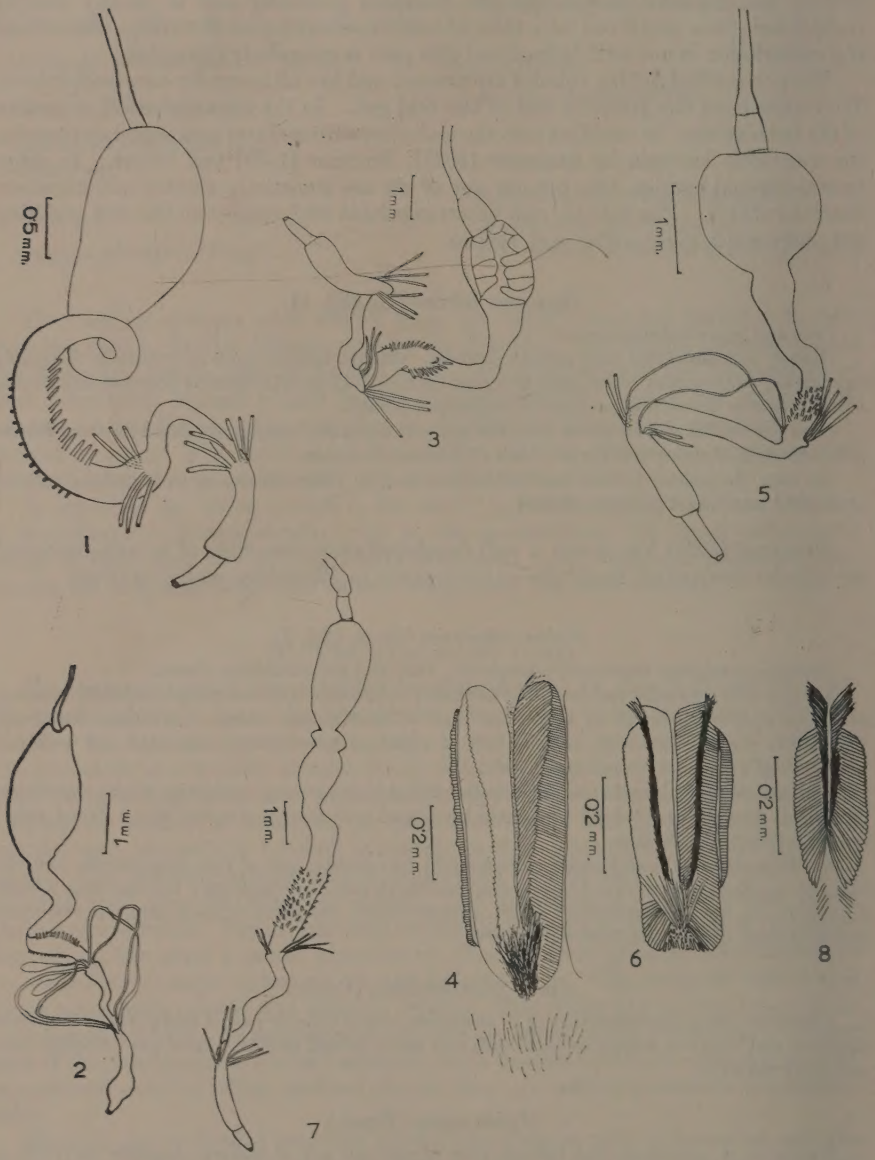
Alimentary canal resembles that of *A. miniatum*, except tubular part of mid gut not of uniform diameter and with 5–6 enteric caeca in each row much behind middle. Hind gut narrower than mid gut anteriorly.

Apion ulicis (Forst.)

Similar to *A. miniatum*, but tubular part of mid gut not of uniform diameter and with 2 enteric caeca, one at a distance from the other ; four Malpighian tubules on one side and two on the other.

Apion radiolus Kirby

Alimentary canal resembles that of *A. miniatum*, but tubular part not of uniform diameter and with only 2 long enteric caeca, one on either side much behind middle ; hind gut narrower anteriorly than mid gut ; two small, almost ovoidal, dumb-bell-shaped Malpighian tubules.



FIGS. 1–8.—(1–3) Alimentary canal of: (1) *Deporaus betulae*; (2) *Apion miniatum*; (3) *Otiorrhynchus singularis*. (4) Proventricular blade of *O. singularis*. (5, 6) *Myllocerus* sp. nov.: (5) alimentary canal; (6) proventricular blade. (7, 8) *Phyllobius pyri*: (7) alimentary canal; (8) proventricular blade.

Apion immune Kirby

Similar to *A. miniatum*, but mid gut with distended part tubular and not indented, tubular part with 4–7 enteric caeca ; hind gut narrower than mid gut at junction, narrowed to posterior flexure.

Phelp (1956) has shown, in *Piezotrachelus varium* Wag. and *Apion chiridanum* Wag., the arrangement of Malpighian tubules, and this is similar to that observed by me in *A. miniatum*.

Otiorrhynchus singularis (L.) (fig. 3)

Oesophagus without crop ; proventriculus (fig. 4) well developed and large, without grinding plates ; blade well defined, unpaired and rounded anteriorly ; retaining bristles numerous, fine and more than one-third length of blade ; declivity teeth absent ; brushes of blade well developed and present on its entire length ; medians not marked anteriorly and with very small hairs and a posterior brush of longer hairs projecting into the cardiac valve ; blades jointly notched at intermedians ; external intermedial fringe not reaching anterior end of blade ; posterior part of oesophagus with irregularly scattered bristles ; cardiac valve without bristles.

Mid gut with its distended part ovoid, wrinkled and without enteric caeca or symbiont-containing structures ; tubular part not of uniform diameter but narrower anteriorly and with numerous enteric caeca, only on one side, behind middle, arranged in three groups.

Hind gut coiled, almost as broad at anterior end as mid gut, narrowed to the posterior flexure, behind which it again broadens before abruptly contracting and continuing as a uniform tube to anus.

Six long Malpighian tubules, inserted anteriorly in two groups, one of four in the projecting part and the other of two ; applied in a group of three tubules on each side of hind gut, behind posterior flexure.

Tissot (1938) studied the alimentary tract in *Naupactus leucoloma* Boh. and my observations broadly agree with his.

Myllocerus sp. nov. (fig. 5)

Oesophagus gradually broadened posteriorly but without distinct crop ; proventriculus (fig. 6) well developed, with rudiments of grinding plates marked by some tubercles in front of median and sieves of declivity broken ; grinding structure well defined anteriorly, slightly concave and unpaired ; retaining bristles fine, pointed and less than one-third the total length of blade ; declivity teeth absent ; brushes of blade almost on its entire length ; medians not marked anteriorly and with small tubercles and a posterior brush of hairs directed towards the cardiac valve ; grinding structures with a small notch at intermedians ; external intermedial fringe almost reaching both ends ; posterior part of oesophagus with short bristles ; cardiac valve without bristles.

Mid gut with distended part ovoid, smooth, but with longitudinal depressions, and without enteric caeca or symbiont-containing structures ; tubular part narrow anteriorly and broad posteriorly, latter part with numerous enteric caeca all round except for a bare longitudinal strip.

Hind gut coiled twice, narrow and of uniform diameter up to posterior flexure, behind which it gradually broadens and then abruptly contracts to form a uniform tube to the anus.

Six long Malpighian tubules, inserted anteriorly in two groups, one group of four entering a projecting part of mid gut, the other two tubules entering separately ; two tubules from the group of four and one of the others applied to hind gut just before last flexure, thus making a group of three on each side.

Myllocerus maculosus Desb.

Agrees with the above species, but proventriculus with retaining bristles short, flat and much less than one-third length of grinding structure ; medians without tubercles or posterior brush of hair ; posterior part of oesophagus without bristles ; mid gut with distended part without longitudinal depressions ; tubular part narrow at both ends and broad in between ; the four Malpighian tubules entering the smaller chamber anteriorly thicker than the other two.

Phyllobius pyri (L.) (fig. 7)

Oesophagus enlarged posteriorly to form crop ; proventriculus (fig. 8) narrow and weakly developed, without grinding plates ; grinding blades paired, weakly developed, narrowed and not defined anteriorly ; retaining bristles absent ; declivity teeth absent ; brushes of blade present throughout its length but narrow and pointed ; medians marked through length of blade and without hairs ; blade notched at intermedians ; external intermedial fringe absent ; crop and cardiac valve without bristles.

Mid gut with distended part oblong, smooth and without enteric caeca ; tubular part with two broad chambers, separated by constriction, anteriorly followed by a region of almost uniform diameter ; enteric caeca numerous and scattered on less than posterior half.

Hind gut narrower than tubular part of mid gut, tubular end of uniform thickness up to application of Malpighian tubules and gradually broadened behind, then contracted into tube of uniform diameter.

Six long Malpighian tubules entering mid gut separately in two groups, one of four and the other of two, applied posteriorly in a group of three on each side.

Phyllobius virideaeris (Laich.)

Agrees with *P. pyri* but proventriculus more developed, blade marked anteriorly and virtually unpaired (faintly paired but not clear) ; retaining bristles short and stout. Tubular part of mid gut without anterior broad chambers with constrictions, and enteric caeca smaller in number and with a longitudinal bare strip.

Jura (1956) observed an almost similar alimentary canal in *Phyllobius glaucus* Stier. to that of *P. pyri*.

Polydrosus tereticollis (DeGeer)

Crop present and broader than the weakly developed proventriculus, latter without grinding plates ; blade continued anteriorly as a narrow and unpaired row of bristles directed backward ; retaining bristles absent ; declivity teeth absent ; brushes of blade on whole of unpaired part, but weakly developed ; medians not marked anteriorly and without any kind of hairs ; blades deeply notched at the intermedians anteriorly ; external intermedial fringe absent ; crop and cardiac valve without bristles.

Mid gut with distended part ovoid, smooth, with a small posterior constriction and without enteric caeca or symbiont-containing structures ; tubular part not of uniform diameter and bearing either two longitudinal groups of three or four rows of enteric caeca on its posterior half.

Hind gut coiled, narrow anteriorly, broader before posterior flexure after which it gradually broadens before abruptly contracting and continuing as a uniform tube to the anus.

Six long Malpighian tubules inserted separately but close to one another ; applied behind posterior flexure in a ventro-lateral group of three on each side.

Strophosomus melanogrammus (Forst.) (fig. 9)

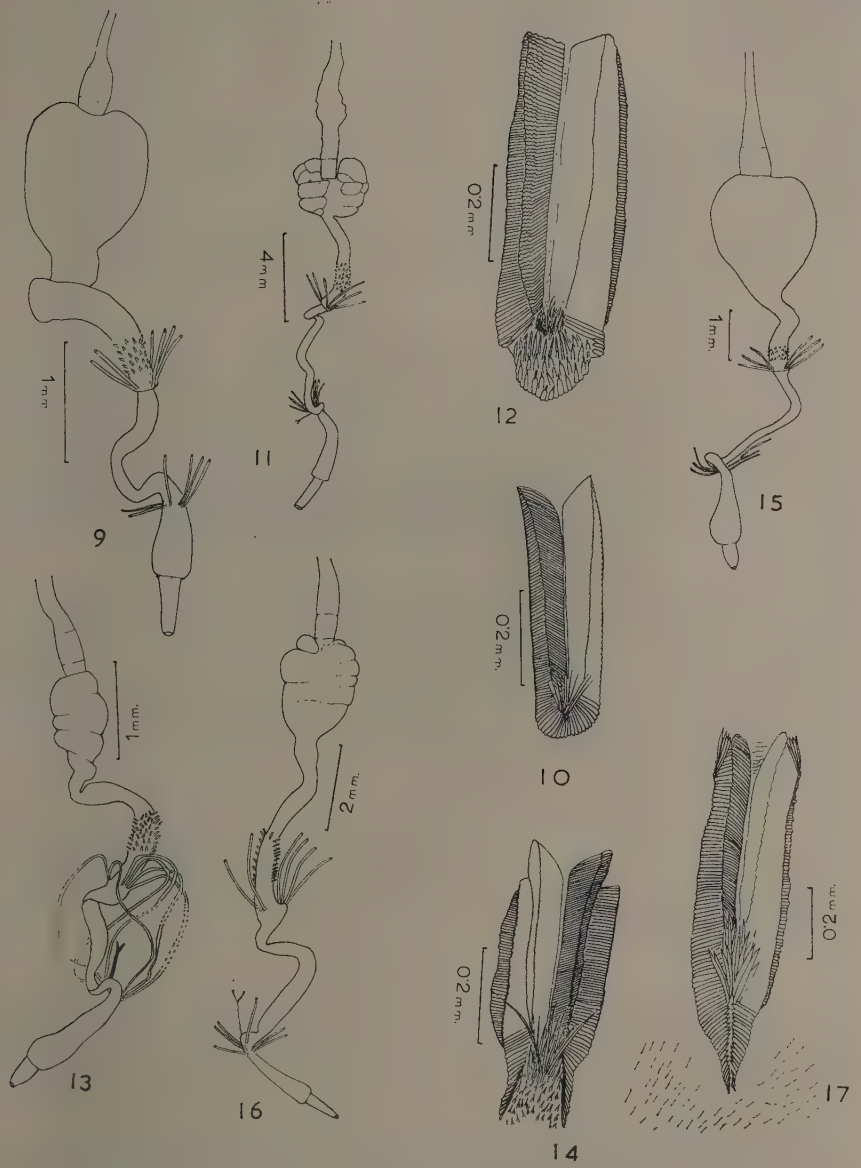
Oesophagus without crop ; proventriculus (fig. 10) well developed, without grinding plates ; blade well defined, unpaired and rounded anteriorly ; retaining bristles broad but pointed apically, one-fifth length of blade ; declivity teeth absent ; brushes of blade well developed ; median not marked anteriorly, without hairs ; blade slightly notched at intermedians ; external intermedial fringe almost as long as blade ; posterior part of oesophagus with scattered bristles, cardiac valve without them.

Mid gut with distended part ovoid, smooth and without enteric caeca or symbiont-containing structures ; tubular part not of uniform diameter and bearing numerous enteric caeca on one side, arranged irregularly near posterior part.

Hind gut coiled, tubular and gradually enlarged behind posterior flexure before being contracted into a narrow tube leading to the anus.

Six long Malpighian tubules inserted separately in two groups, one of four and the other of two ; applied posteriorly in three groups each of one, two and three behind the posterior flexure.

Chorabik (1952) studied the digestive system in *Strophosmus capitatus* Deg. which almost resembles the description above.



FIGS. 9–17.—(9, 10) *Strophosomus melanogrammus*: (9) alimentary canal; (10) proventriculus (11, 12) *Parisomias* sp. nov.: (11) alimentary canal; (12) proventricular blade.. (13, 14) *Amblyrrhinus subrecticollis*: (13) alimentary canal; (14) proventricular blade. (15) Alimentary canal of *Sitona regensteinensis*. (16, 17) *Hypolixus truncatulus*: (16) alimentary canal; (17) proventricular blade.

Parisomias sp. nov. (fig. 11)

Oesophagus short; crop large and sclerotised; proventriculus (fig. 12) well developed but almost parallel sided, with unpaired grinding plate, less than one-sixth length of blade, rounded, well defined anteriorly and with scaly structures, each structure with a thick pointed tubercle; retaining bristles short, pointed and less than one-fourth length of blade; median with minute hairs; grinding structure notched at intermedians; external intermedial fringe continued up to posterior end but not up to notch; crop with a large number of irregularly arranged bristles; cardiac valve without bristles.

Mid gut with distended part ovoid, strongly lobed, probably carrying symbionts but without enteric caeca; tubular part narrow anteriorly, broader posteriorly and with numerous thinly scattered enteric caeca all round posterior half.

Hind gut coiled and long; narrow anteriorly, gradually broadened behind posterior flexure, and then abruptly contracted into a tube.

Six long Malpighian tubules inserted separately in two groups, one of four and the other of two; applied separately under posterior flexure.

Amblyrrhinus subrecticollis Marsh. (fig. 13)

Oesophagus slightly broadened posteriorly and without crop; proventriculus (fig. 14) well developed and slightly rounded on sides, with unpaired short grinding plates surrounded on both sides by the declivities, irregularly defined anteriorly; plate with scaly structures, each with an apical tubercle; retaining bristles flat and not reaching middle of blade; declivity teeth absent; brushes of blade on entire length and well developed; median not marked throughout grinding structure and without hairs or posterior projected brush of hairs; grinding structures narrow anteriorly and deeply notched at intermedians; external intermedial fringe present between anterior notch and posterior end; posterior part of oesophagus with short irregularly scattered bristles; cardiac valve without bristles.

Mid gut with distended part ovoid, lobed in female and smooth in male, and without enteric caeca; tubular part not of uniform diameter and with numerous enteric caeca on posterior part, leaving a smooth longitudinal strip.

Hind gut coiled, broad anteriorly and narrowed to the posterior flexure, behind which broadening before abrupt posterior contraction; tube short.

Six Malpighian tubules inserted separately in two groups anteriorly, one of four long tubules, the other of two short, narrow ones; applied posteriorly in two groups of three each, each group comprising two long and one short tubule.

Amblyrrhinus sp. nov.

Agrees with *A. subrecticollis* except that there are enteric caeca on the mid gut all round the tubular part, without a smooth strip and the hind gut is narrow up to the posterior flexure.

Sitona regensteinensis (Hbst.) (fig. 15)

Oesophagus without crop; proventriculus well developed, without grinding plate but with some short and stout bristles; blades unpaired and weakly defined anteriorly; retaining bristles narrow, pointed and less than one-fourth the length of the blade; declivity teeth absent; brushes of blades well developed and on entire length; medians diffused anteriorly, with tubercles and a few hairs and tubercles projecting into the cardiac valve; blades very slightly notched at intermedians anteriorly; external intermedial fringe shorter towards both extremities of blade; posterior part of oesophagus with a few scattered bristles; cardiac valve without bristles.

Mid gut with distended part ovoid, smooth and without enteric caeca or symbiont-containing structures; tubular part not of uniform diameter, shorter than hind gut and with a few enteric caeca irregularly arranged and variable in number.

Hind gut longer, coiled, tubular, narrow up to posterior flexure, behind which it gradually broadens before being abruptly contracted to continue as a tube to the anus.

Six long Malpighian tubules inserted separately in a group of three on either side of mid gut, applied separately on latero-ventral side behind posterior flexure.

Sitona sp.

Agrees with *S. regensteinensis* but proventriculus with retaining bristles equal to one-third length of blade ; medians with hairs and tubercles projecting into cardiac valve ; posterior part of oesophagus without bristles ; distended part of mid gut oblong in outline narrowing to both ends ; tubular part with seven enteric caeca in two groups near insertion of Malpighian tubules.

Hypolixus truncatulus Fab. (fig. 16)

Oesophagus strongly sclerotised and slightly broader posteriorly ; crop absent ; proventriculus (fig. 17) well developed and almost parallel-sided, without grinding plates ; blades paired, continuing on both sides of median and narrowing anteriorly into a pointed wedge ; true retaining bristles absent ; medians marked throughout length of blades ; blades notched at intermedians ; declivity sieves continued to apex and declivity teeth absent ; brushes present throughout length of blade, though short and broad anteriorly ; external intermedial fringe present from intermedial notch to posterior end ; medians with neither hair nor a brush of longer hair projecting into cardiac valve ; posterior part of oesophagus with a large number of scattered bristles ; cardiac valve without bristles.

Mid gut with distended part ovoid and lobed (the lobes may carry symbionts) ; tubular part longer than preceding part, not of uniform diameter and with numerous enteric caeca around posterior part at some distance from Malpighian tubules ; posterior part projecting to form a chamber on one side.

Hind gut tubular, coiled, narrow before posterior flexure, broadened posteriorly and again contracting into a finger-like tube leading to the anus.

Six Malpighian tubules inserted into mid gut in three groups, four tubules into a common chamber, another tubule entering dorsally and the last one ventrally ; at posterior flexure one applied dorsally behind ligament of ovaries, one ventrally and two on each side.

Conorhynchus brevirostris Gyll. (fig. 18)

Oesophagus sclerotised ; crop elongate ; proventriculus well developed and parallel-sided, without grinding plates ; blades paired, very narrow anteriorly and not well defined ; retaining bristles absent (broad brushes in two rows may be mistaken for bristles) ; declivity teeth absent ; brushes of blade broad and short anteriorly but present throughout ; medians marked throughout and with hairs but no projecting brush behind ; blades deeply notched anteriorly at intermedians ; external intermedial fringe up to anterior incision ; crop with scattered bristles ; cardiac valve without bristles.

Mid gut with distended part strongly wrinkled, ovoid and without enteric caeca ; tubular part not of uniform diameter and with enteric caeca all round posteriorly ; posterior chamber less marked.

Hind gut similar to that of *Hypolixus truncatulus*.

Six Malpighian tubules inserted anteriorly as in *Hypolixus* ; applied at posterior flexure in a group of three on one side, a group of two on the other and one dorsally.

Xanthochelus faunus Ol.

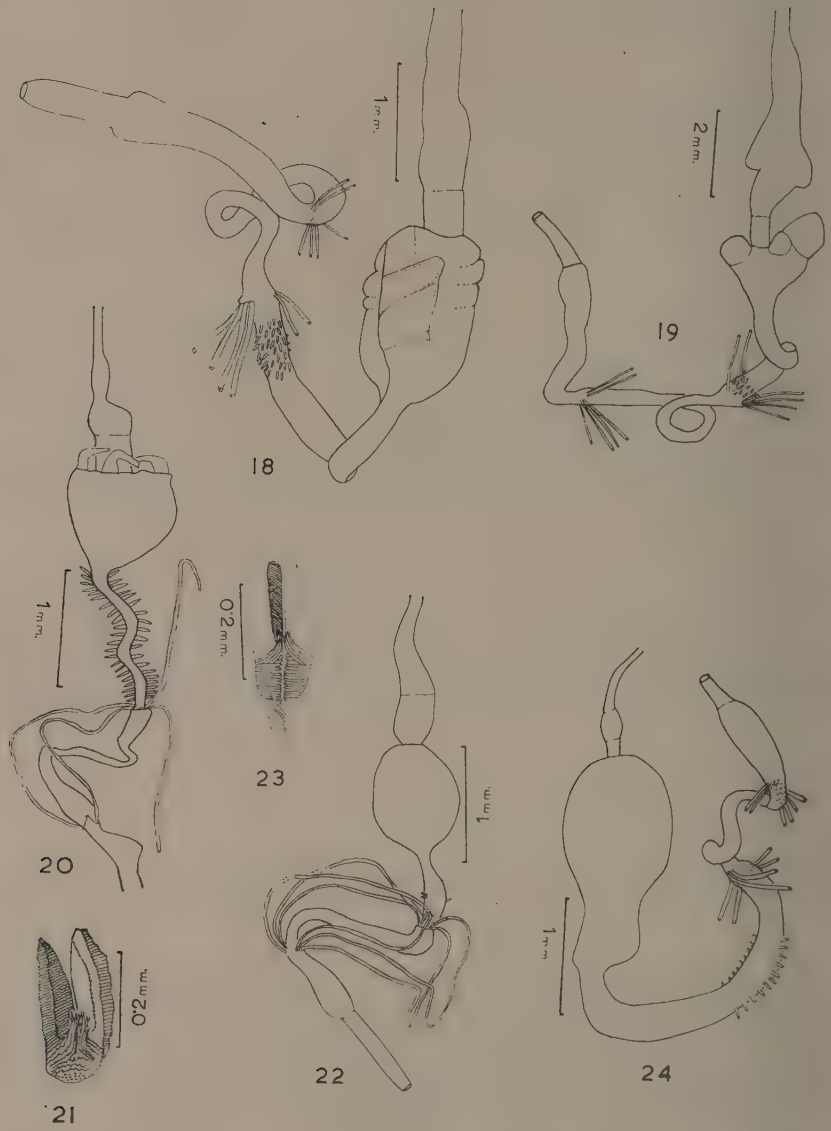
Oesophagus sclerotised and with large crop ; proventriculus rounded on sides and well developed, similar to *Conorhynchus*, except brushes of blade very long and a little behind anterior tip (they may be mistaken for retaining bristles).

Mid gut similar to *Conorhynchus* except tubular part with enteric caeca all round behind middle, leaving a bare part towards Malpighian tubules ; posterior chamber well marked.

Hind gut and Malpighian tubules as in *Conorhynchus*.

Neocleonus sanio Hbst. (fig. 19)

Oesophagus sclerotised, with large crop ; proventriculus well developed, similar to *Conorhynchus* except blade not narrow, but rounded anteriorly ; blades broadly notched at intermedians. Mid gut with nodule-like symbiont-carrying structures on anterior of distended part (only one female seen) ; tubular part with fewer enteric caeca scattered all round on a short posterior part only. Hind gut long, coiled and broadened from anterior to posterior flexure behind which similar to *Conorhynchus*. Malpighian tubules as in *Conorhynchus*.



FIGS. 18–24.—(18–20) Alimentary canal of: (18) *Conorhynchus brevirostris*; (19) *Neocleonus sanio*; (20) *Pentarthrum huttoni*. (21) Proventricular blade of *P. huttoni*. (22, 23) *Bagous* sp.: (22) alimentary canal; (23) proventricular blade. (24) Alimentary canal of *Dorytomus tortrix*.

Pentarthrum huttoni Woll. (fig. 20)

Oesophagus enlarged to form a crop ; proventriculus (fig. 21) well developed, with unpaired grinding plate having cross rows of tubercles anteriorly followed by serrations ; blades with broad retaining bristles ; declivity teeth absent ; brushes of blade very short and serrated apically ; blades notched at medians posteriorly but hardly so at intermedians anteriorly ; crop with scattered bristles ; cardiac valve without bristles.

Mid gut with distended part ovoid, smooth, with six large enteric caeca all round anterior margin ; tubular part with two rows of enteric caeca on entire length.

Hind gut broader near insertion and application of Malpighian tubules than between them.

Four Malpighian tubules inserted in one group anteriorly, two applied posteriorly, one on each side and the other two free.

Chararas (1956) gave an account of the alimentary canal (including proventriculus) of *Rhyncolus porcatus* Germ., *R. elongatus* Gyll., *Pentarthrum huttoni* Woll. and *Caulotrupis aeneopiceus* Boh. He observed eight enteric caeca on the distended part of the mid gut in *Rhyncolus* and six in the others. He also noted four Malpighian tubules in *R. elongatus* and *Pentarthrum huttoni* and six in the others. My observations differ in that *P. huttoni* has two free tubules whereas Chararas has shown a crypto-nephridic condition in all.

Bagous sp. (fig. 22)

Oesophagus distended posteriorly to form crop ; proventriculus (fig. 23) well developed, characteristic ; blade with declivity sieves faint, marked up to the long brushes and declivities with transverse lines anteriorly and short brushes (may be mistaken for grinding plate) ; blades well defined, truncate anteriorly and paired ; retaining bristles absent ; declivity teeth absent ; brushes of blade long only on a little more than half the blade and serrated apically, then continued as two rows of short tubercles anteriorly ; median marked throughout ; blade narrow anteriorly and deeply notched at intermedians ; external intermedial fringe not clear ; crop with a row of long bristles in front of each median ; cardiac valve without bristles.

Mid gut with distended part ovoidal, smooth and without enteric caeca or symbiont-containing structures ; tubular part not of uniform diameter, narrow anteriorly and broad posteriorly, much shorter than hind gut, with 1–2 enteric caeca on either side.

Hind gut broad at junction with mid gut, then narrowed to posterior flexure behind which it enlarges before contracting into a narrow tube.

Six Malpighian tubules inserted anteriorly in two groups, one of four long tubules, the other of two short ones ; applied behind posterior flexure in a group of three, two long and one short, on either side.

Dorytomus tortrix (L.) (fig. 24)

Oesophagus long ; crop absent ; proventriculus well developed externally and rounded on sides, grinding plates absent ; blade clearly defined, rounded and unpaired anteriorly ; retaining bristles fine, pointed and reaching less than one-fourth length of blade ; median without hairs or a brush of long projecting hair ; declivity teeth absent ; brushes of blades on entire length of blade ; blade less notched at intermedians anteriorly ; external intermedial fringe present ; oesophagus with long and scattered bristles ; cardiac valve without bristles.

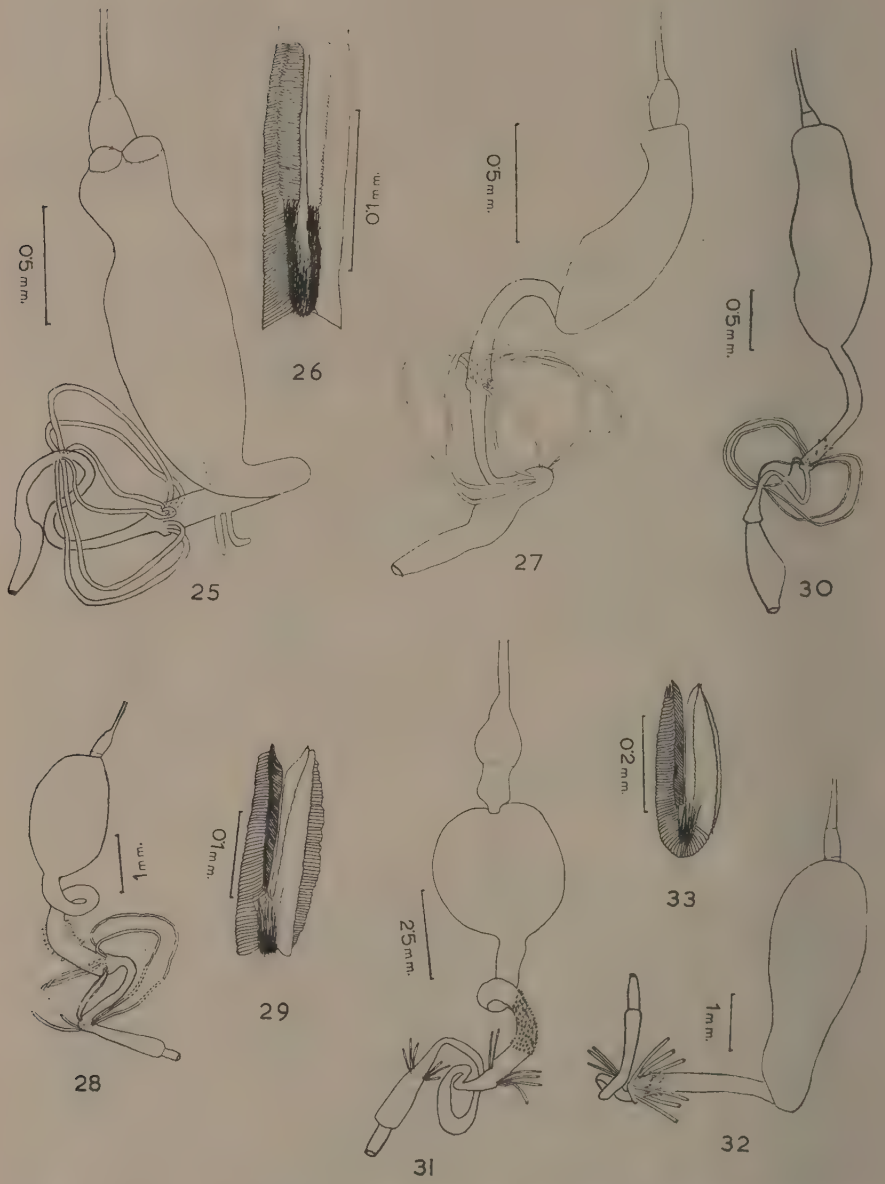
Mid gut with distended part ovoid, smooth and without enteric caeca or symbiont-containing structures ; tubular part broad anteriorly, with two rows, each of 8–11 enteric caeca, behind middle but at a little distance from insertion of Malpighian tubules.

Hind gut coiled and shorter than tubular mid gut, narrow up to posterior flexure, after which narrowed and again contracted into a tube leading to the anus.

Six Malpighian tubules separately inserted in two groups, one of four long tubules, the other of two short ones ; applied separately in one group at posterior flexure.

Dorytomus rufatus (Bed.)

Similar to *D. tortrix* but proventriculus with retaining bristles reaching one-third length of blade. Mid gut with tubular part narrow anteriorly ; each row with 8–9 enteric caeca. Six Malpighian tubules inserted anteriorly in two groups, one of four long tubules, the other of two short ones ; applied on sides of posterior flexure in a group of three on each side, two long and one short.



Figs. 25–33.—(25, 26) *Miccotrogus picirostris*: (25) alimentary canal; (26) proventricular blade. (27) Alimentary canal of *Sibinia arenariae*. (28, 29) *Anthonomus pedicularius*: (28) alimentary canal; (29) proventricular blade. (30-32) Alimentary canal of: (30) *Balanobius pyrrhoceras*; (31) *Hylobius abietis*; (32) *Hypera murina*. (33) Proventricular blade of *H. murina*.

Dorytomus dejeani (Fst.)

Similar to *D. tortrix* but proventriculus with retaining bristles about one-third length of blade. Mid gut with narrow tubular part anteriorly; each row with 6–12 enteric caeca. Hind gut narrow at anterior end and posterior flexure, broad in between. Malpighian tubules as in *D. rufatus*.

Miccotrogus picirostris (Fab.) (fig. 25)

Oesophagus long; crop absent; proventriculus (fig. 26) well developed internally, without grinding plates; blade undefined and unpaired anteriorly; retaining bristles fine and about one-fourth length of blade; medians not marked anteriorly and with neither hairs nor a brush of hairs projecting into the cardiac valve; declivity teeth absent; brushes short and serrated internally; blades not notched at intermedians anteriorly; external intermedial fringe transversely striate and apparently serrated apically on entire length; posterior part of oesophagus and cardiac valve without bristles.

Mid gut with distended part long, on the whole smooth, notched anteriorly, nodules probably symbiont-carrying, then narrowing and again broadening; without enteric caeca; tubular part shorter than preceding part, of uniform breadth, with one or two long caeca on each side behind middle (two or three caeca in all).

Hind gut reverse S-shaped, tubular, abruptly distended rectum lying applied to anterior bend of S.

Six Malpighian tubules inserted in three groups anteriorly, a group of two long tubules on each side and one group of two short tubules dorsally; applied at posterior flexure, three on either side, two long and adjacent one short.

Sibinia arenariae Steph. (fig. 27)

Proventriculus as in *Miccotrogus*, except brushes of blades long and not serrated internally; intermedial fringe not distinct; posterior part of oesophagus with bristles; mid gut similar to that of *Miccotrogus* except no nodules on anterior distended part; tubular part with one enteric caecum near its posterior end. Hind gut similar to that of *Miccotrogus*. Six Malpighian tubules similar to those of *Miccotrogus* in size and arrangement.

Anthonomus pedicularius (L.) (fig. 28)

Oesophagus long; crop absent; proventriculus (fig. 29) elongate and weakly developed, without grinding plates; blades unpaired, slightly rounded and narrow anteriorly; retaining bristles thin, pointed and reaching about one-third length of blade; declivity teeth absent; brushes of blade on entire length; median not marked anteriorly and without hairs or a brush of hairs projecting behind; intermedians continued up to both ends of blade, which is therefore not notched; external intermedial fringe in the form of transverse striations, shorter on both extremities; posterior part of oesophagus with some stout bristles; cardiac valve without bristles.

Mid gut with distended part smooth, ovoid and without enteric caeca or symbiont-containing structures; tubular part not of uniform diameter, broad posteriorly and carrying two rows each of 6–9 enteric caeca, behind middle but some distance from posterior end.

Hind gut tubular, narrow, but slightly broadened behind posterior flexure and then abruptly contracted into a narrow tube.

Six Malpighian tubules inserted anteriorly in two groups, one of four long tubules, the other of two short ones; applied at posterior flexure in three groups, two long tubules on each side and two short ones dorsally.

The observations of Miles (1923), on *A. pomorum* L., and Vukašovic (1932) are similar to mine on *A. pedicularius* L.

Anthonomus inversus Bed.

Similar to *A. pedicularius* except that the tubular part of the mid gut is thicker anteriorly and each row bears 6–10 enteric caeca.

Balaninus glandium Marsh.

Oesophagus long; crop absent; proventriculus well developed, without grinding plates; blades unpaired and slightly projecting at medians leaving the declivities behind; retaining bristles narrow, pointed and reaching about one-fourth length of blade; declivity teeth absent; brushes of blade on entire length; medians without hairs and declivity with a brush of long hairs projecting into cardiac valve; intermedians projecting anteriorly; external intermedial fringe transversely striate; bristles in oesophagus longer in continuation of medians, shorter and scattered between these rows; cardiac valve without bristles.

Mid gut with distended part wrinkled, oblong or flask-shaped and without enteric caeca or symbiont-containing structures; tubular part not of uniform thickness, with enteric caeca irregularly arranged on a short part near posterior end.

Hind gut longer and for the most part narrower than mid gut, gradually enlarged behind posterior flexure, then abruptly contracted to a narrow or large conical tube.

Six long Malpighian tubules inserted anteriorly in four groups; two groups of two each slightly separated from one another and two single tubules more separated than the other two groups; applied in a group of three on each side of posterior flexure.

Balaninus venosus (Grav.)

Similar to *B. glandium* except proventriculus with blades not projecting in front of declivities; bristles in oesophagus long and scattered. Six Malpighian tubules inserted in two groups, one of four tubules, the other of two; applied at posterior flexure in a group of three on each side.

Balanobius pyrrhoceras Marsh. (fig. 30)

Oesophagus long and narrow; crop absent; proventriculus weakly developed, without grinding plates; blade paired and notched anteriorly; retaining bristles absent; declivity teeth absent; brushes of blade weakly developed but present on entire length of blade; medians marked throughout, without hairs and with a projecting brush of hairs behind; a brush of hairs projecting behind intermedians; external intermedial fringe present; oesophagus with scattered bristles; cardiac valve without bristles.

Mid gut with distended part tubular or flask-shaped, smooth and without enteric caeca or symbiont-containing structures; tubular part of uniform diameter, shorter than preceding part and carrying 6–9 enteric caeca irregularly arranged posteriorly.

Hind gut narrow, S-shaped, broader behind posterior flexure, then abruptly contracting but expanding into a sac again.

Six Malpighian tubules inserted anteriorly in two groups, one of four long tubules, the other of two short ones; applied behind posterior flexure in a group of three on each side, two long and one short.

Balanobius salicivorus Payk.

Similar to *B. pyrrhoceras* except that the mid gut has 4–7 enteric caeca on the tubular part.

Hylobius abietis L. (fig. 31)

Crop present; proventriculus well developed, without grinding plates; blade narrow anteriorly and continued as unpaired row of bristles; retaining bristles short and fine; declivity teeth absent; brushes of blade well developed and present throughout length of blade; medians not marked anteriorly, hairs present in median and brush of hair projecting into cardiac valve, an additional brush also present in the valve at intermedians; blade notched at intermedians anteriorly; external intermedial fringe not reaching anterior incision; crop with two rows of long bristles, one a continuation of median and the other of intermedian; cardiac valve without bristles.

Mid gut with distended part smooth, with only a longitudinal depression on either side, ovoid and without enteric caeca or symbiont-containing structures; tubular part not of uniform diameter, with numerous irregularly arranged enteric caeca attached just ahead of Malpighian tubules.

Hind gut narrow anteriorly, gradually broadened behind posterior flexure and then abruptly contracted and continued as a narrow tube.

Six long Malpighian tubules inserted in two groups, one of four and the other of two; applied separately, laterally and ventrally, behind the posterior flexure.

Hypera murina (Fab.) (fig. 32)

Oesophagus long and slightly broader posteriorly; crop absent; proventriculus (fig. 33) moderately developed and longer than broad, without grinding plates; blade well defined, unpaired and rounded anteriorly; retaining bristles fine and less than one-third length of blade; declivity teeth absent; brushes of blade on entire length and well developed; medians not marked anteriorly and without hairs or a brush of long hairs projecting into cardiac valve; blades notched anteriorly at intermedians; external intermedial fringe not transversely striate; posterior part of oesophagus with scattered bristles; cardiac valve without bristles.

Mid gut oblong, gradually narrowing, without enteric caeca; smooth in male, wrinkled and with nodules in female; tubular part not of uniform diameter, shorter than distended part and bearing variable number of irregularly arranged enteric caeca on short length near Malpighian tubules.

Hind gut coiled, narrower than its preceding part, gradually broadened behind the posterior flexure and abruptly contracted into a narrow tube.

Six long Malpighian tubules inserted all round anteriorly; applied at the posterior flexure in a group of three on either side.

Stammer (1934) has also shown the same arrangement of Malpighian tubules in the genus *Phytonomus* (*Hypera*).

Hypera punctata (Fab.)

Similar to *H. murina* except that the proventriculus has retaining bristles reaching less than one-fifth the length of the blade.

Gronops lunatus (Fab.) (fig. 34)

Oesophagus tubular; crop absent; proventriculus (fig. 35) developed but slightly rounded on sides, without grinding plates; blades faintly defined anteriorly but subtruncate and unpaired; retaining bristles fine and longer than one-third but shorter than half length of blade; declivity teeth absent; brushes of blade continued up to anterior extremity; medians without hairs or a brush of long hairs projecting into cardiac valve; blades not notched at intermedians anteriorly; external intermedial fringe absent; posterior part of oesophagus with irregularly scattered bristles; cardiac valve without bristles.

Mid gut with distended part oblong, gradually narrowed posteriorly, smooth and without enteric caeca or symbiont-containing structures; tubular part broad anteriorly, shorter than preceding part, with 1–2 enteric caeca on either side, very close to posterior end.

Hind gut longer than preceding tubular part, slightly broadened behind posterior flexure but abruptly constricted into a finger-like tube.

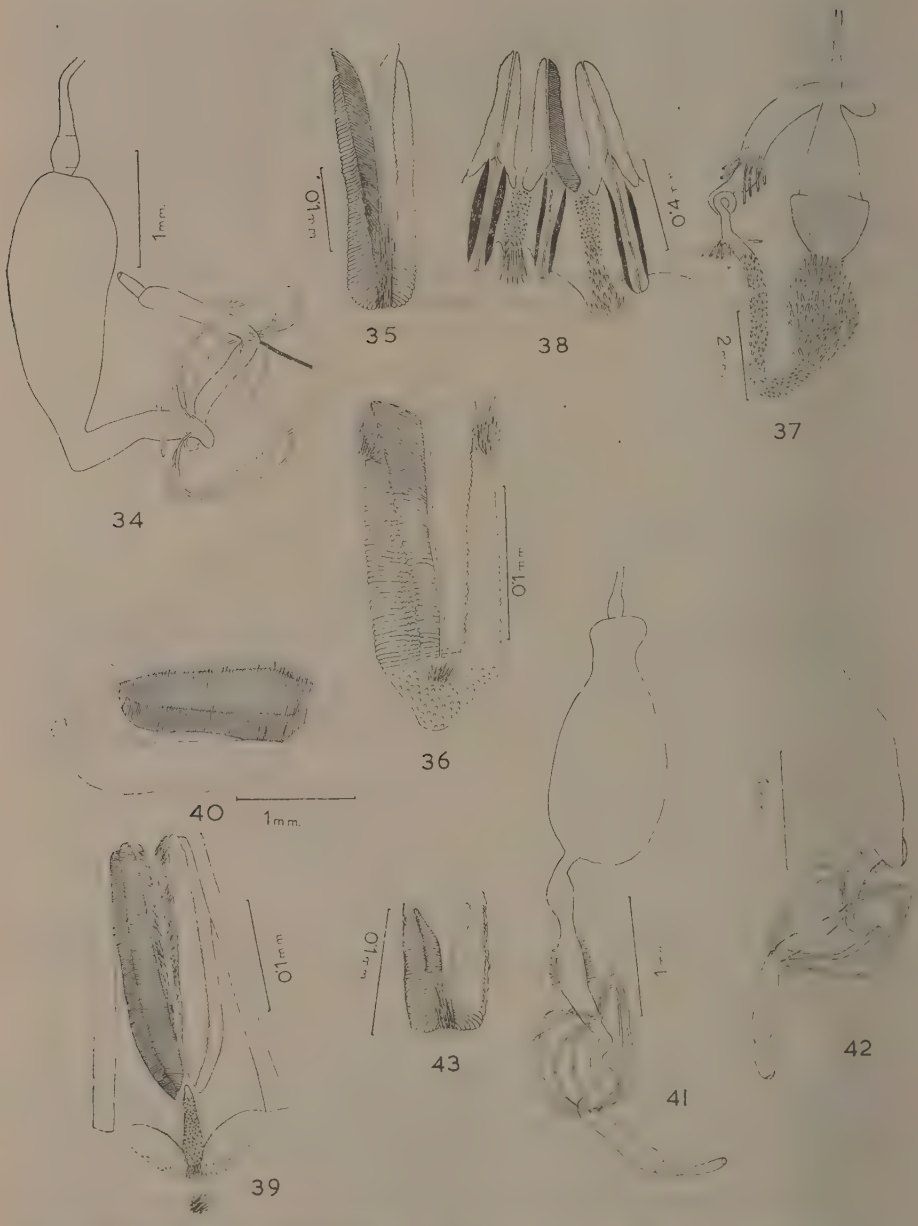
Six Malpighian tubules inserted in two lateral and one ventral group of two tubules each, former groups of long tubules and latter of short ones; applied at the posterior flexure in three groups, two tubules in each group; differing from *Miccotrogus* in that the three adjacently inserted tubules are applied at the flexure on the opposite side, the tubules therefore crossing.

Sitophilus oryzae (L.)

Crop present; proventriculus (fig. 36) strongly developed and rounded on sides, with short triangular grinding plates, each plate with scaly tubercular structures, unpaired, abruptly narrowed and rounded anteriorly, well defined from crop; blade much longer than grinding plate; retaining bristles short, sharply pointed and brush-like; declivity teeth present as an upper longitudinal row on declivities; brushes stout, projecting back into cardiac valve and untoothed internally; medians without hairs or a posterior brush of projecting hairs; a brush of hairs projecting into cardiac valve at intermedians; external intermedial fringe present, not transversely striate; crop with scattered bristles; cardiac valve without bristles.

Mid gut with a large number of scattered enteric caeca, longer on distended part than on tubular part; distended part ovoid.

Hind gut coiled, gradually broadened behind posterior flexure then contracted slightly to form a tube leading to anus and a small muscular flap present up to less than half posterior tube; this flap not found in other species studied previously.



FIGS. 34–43.—(34, 35) *Gronops lunatus*: (34) alimentary canal; (35) proventricular blade. (36) Proventricular blade of *Sitophilus oryzae*. (37, 38) *Cosmopolites sordidus*: (37) alimentary canal; (38) proventricular blade. (39, 40) Proventricular blade of *Rhynchophorus* sp. (41) Alimentary canal of *Coeliodes rubicundus*. (42, 43) *Micrelus ericae*: (42) alimentary canal; (43) proventricular blade.

Six Malpighian tubules inserted in a common chamber on one side ; applied under the posterior flexure in one group.

Murray and Tiegs (1935) have similar observations on the gross anatomy of the alimentary canal of *S. oryzae*.

Cosmopolites sordidus Aur. (fig. 37)

Oesophagus narrow anteriorly and distended posteriorly to form a stout muscular crop ; proventriculus (fig. 38) strongly developed, broad anteriorly and narrow towards cardiac valve, grinding plates with scaly raised area and plain longitudinal slopes, four plates with large tubular prominences posteriorly and short, broad scaly structures, remainder with small prominences and long, broad structures directed anteriorly in addition to small scaly ones in all ; each plate V-shaped at base ; blades notched at medians, brushes of adjoining blades thus meeting at intermedians and without declivity sieves ; retaining bristles absent ; declivity teeth absent ; brushes on entire length of blade ; median broad and without hairs ; grinding structures at intermedians with intermedial flanges of plates projecting into crop, thus dividing the anterior notch into two parts ; external intermedial fringe flap-like and not striated ; crop with a row of long bristles in front of each median, short row in continuation of intermedians and scattered short, stout bristles throughout ; cardiac valve without bristles.

Rhynchophorus sp.

Similar to *Cosmopolites* but proventriculus (figs. 39 and 40) with all grinding plates having tubercular prominences and short scales, plane slopes continued on lateral sides of declivities ; each plate broadly V-shaped and with small broad bristles anteriorly ; blades not notched at medians posteriorly ; declivity sieves present ; grinding structures jointly emarginate at intermedians, intermedial flanges of plate less developed. Mid gut with tubular part very long, Malpighian tubules inserted on one side, four in a projecting chamber and one on each side of the chamber separately ; posterior application not seen.

Coeliodes rubicundus (Hbst.) (fig. 41)

Crop absent ; proventriculus weakly developed and small, without grinding plates ; blades unpaired and undefined anteriorly ; retaining bristles fine and pointed ; declivity teeth absent ; brushes short and extended over almost entire length of blade ; medians without hairs ; blades not marked at intermedians ; external intermedial fringe visible as a serrated structure ; posterior part of oesophagus with scattered bristles ; cardiac valve without bristles.

Mid gut with distended part oblong or flask-shaped, smooth and without enteric caeca or symbiont-containing structures ; tubular part not of uniform diameter and with two rows each of 7–9 enteric caeca, leaving a smooth part of the gut in front and behind.

Hind gut not of uniform diameter on anterior part before posterior flexure, normally broadened and contracted into a tube behind flexure.

Six Malpighian tubules inserted anteriorly in two groups, one of four long tubules, the other of two short ones ; applied at posterior flexure in a group of three on each side, each of two long tubules and one short one.

Rozsypal (1941) has shown that the alimentary canal in *Stenocarus fuliginosus* Marsh. is similar to that of *Coeliodes rubicundus*.

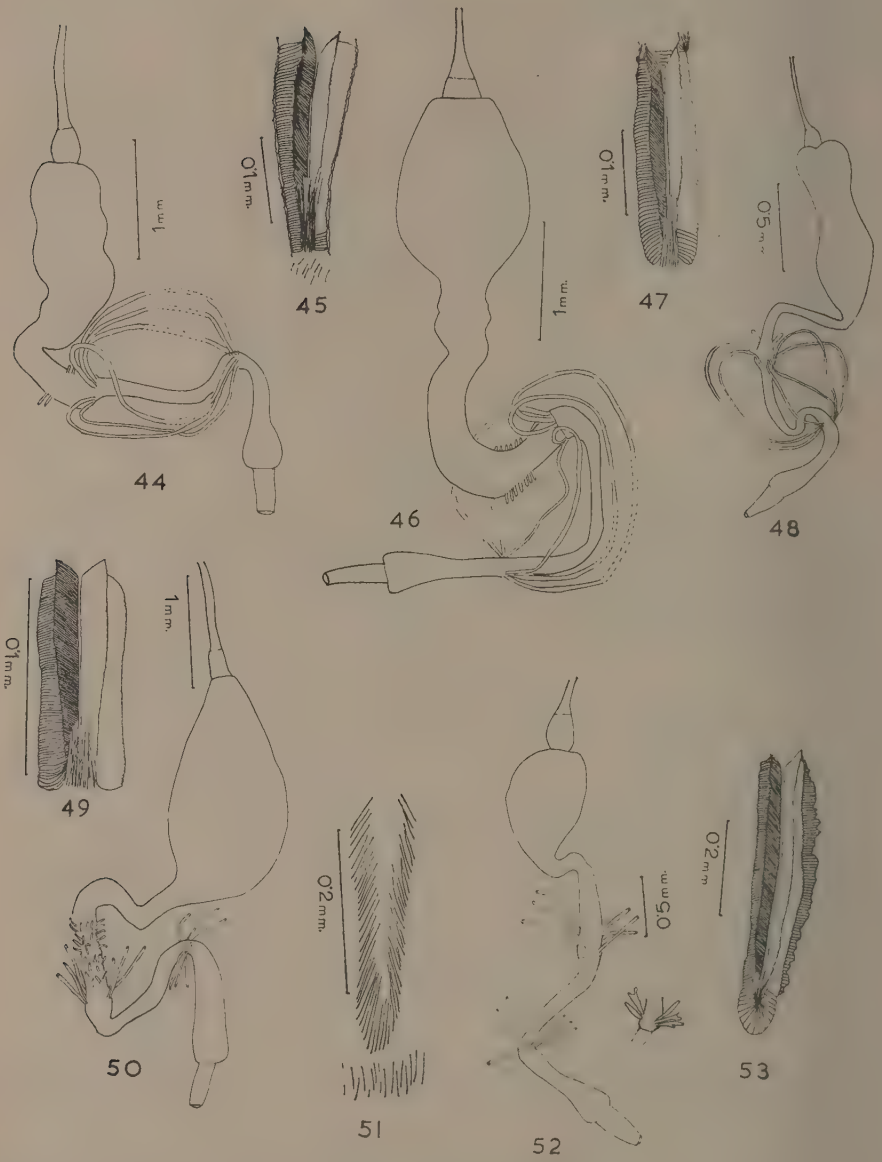
Micrelus ericae (Gyll.) (fig. 42)

Crop absent ; proventriculus (fig. 43) weakly developed, similar to that of *Coeliodes* except that each blade is relatively broader, not defined, but somewhat concave anteriorly ; intermedians projecting ; blades notched at medians posteriorly.

Mid gut similar to that of *Coeliodes* except that tubular part is of uniform diameter and each row has 5–9 enteric caeca.

Hind gut of almost uniform diameter up to posterior flexure and similar to that of *Coeliodes* thereafter.

Malpighian tubules as in *Coeliodes*.



FIGS. 44–53.—(44, 45) *Cidnorrhinus quadrimaculatus* : (44) alimentary canal ; (45) proventricular blade. (46) Alimentary canal of *Ceuthorrhynchus pollinarius*. (47) Proventricular blade of *Rhinoncus pericarpius*. (48, 49) *Gymnetron pascuorum* : (48) alimentary canal ; (49) proventricular blade. (50, 51) *Alcidodes fabricii* : (50) alimentary canal ; (51) proventricular blade. (52, 53) *Cionus scrophulariae* : (52) alimentary canal ; (53) proventricular blade.

Cidnorrhinus quadrimaculatus (L.) (fig. 44)

Crop absent; proventriculus (fig. 45) well developed externally, weakly developed internally and without grinding plates; blades unpaired, narrow and not well defined anteriorly; retaining bristles small and fine; declivity teeth absent; brushes of blade weak but present on entire length; medians with short hairs but without the projecting fringe posteriorly; blade not notched at intermedians; external intermedial fringe continued almost to both extremities; posterior part of oesophagus with scattered bristles; cardiac valve without bristles.

Mid gut with distended part tubular or flask-shaped, smooth and without enteric caeca or symbiont-containing structures; tubular part short and with two enteric caeca on each side.

Hind gut tubular, longer than mid gut, broadened behind posterior flexure before being contracted into a tube.

Six Malpighian tubules inserted anteriorly in two groups, one of four long tubules, the other of two short ones; applied at posterior flexure in a group of three on each side (differing from the arrangement shown by Stammer (1934) in that the anterior group of two is applied to one side posteriorly).

Ceuthorrhynchus pollinarius Forst. (fig. 46)

Crop absent; proventriculus small, weak and without grinding plates; blade unpaired and not well defined anteriorly; retaining bristles short and fine; brushes of blades weak on entire length; medians marked throughout with stout hairs and without a brush projecting posteriorly; blades not notched anteriorly at intermedians; external intermedial fringe not clear but instead a wavy line visible; posterior part of oesophagus with bristles; cardiac valve without bristles.

Mid gut with distended part ovoid, smooth and without enteric caeca or symbiont-containing structures; tubular part not of uniform diameter and having two rows each of 6–7 enteric caeca much behind middle.

Hind gut longer than preceding tubular part, broadened behind posterior flexure and then contracted into a tube leading to the anus.

Six Malpighian tubules inserted anteriorly in two groups, one of four long tubules, the other of two short ones, applied behind posterior flexure in a group of three on each side, two long and one short tubule in each group.

Stammer (1934) has shown all tubules long in the genus *Ceuthorrhynchus*; this, apparently, is an oversight.

Gunthart (1949) has studied the digestive system in *C. quadridens* Panz. and *C. napi* Gyll.

Rhinoncus pericarpius (L.)

Crop absent; proventriculus (fig. 47) small, weak on the whole and without grinding plates; blade unpaired and somewhat defined anteriorly; retaining bristles fine and about one-third length of blade; declivity teeth absent; brushes of blade present throughout and notched posteriorly at medians; medians without hairs or a posterior brush of hairs; blades not notched anteriorly at intermedians; external intermedial fringe irregular but continued to both ends; posterior part of oesophagus and cardiac valve without bristles.

Mid gut with oblong and smooth distended part, without enteric caeca or symbiont-containing structures; tubular part not of uniform diameter and with two rows each of 6–14 enteric caeca at about middle.

Hind gut and six Malpighian tubules as in *Ceuthorrhynchus* and not as figured by Stammer (1934) for the genus *Rhinoncus*.

Gymnetron pascuorum (Gyll.) (fig. 48)

Oesophagus tubular; crop absent; proventriculus (fig. 49) small, weakly developed on the whole and without grinding plates; blades unpaired, not defined and concave at median anteriorly; retaining bristles fine and about one-fourth length of blade; declivity teeth absent; brushes of blades present throughout the length; blades not notched at intermedians anteriorly; medians not marked and with neither hairs nor a posterior brush of hair; intermedial fringe present; posterior part of oesophagus with bristles; cardiac valve without bristles.

Mid gut with distended part elongate, shoe-shaped with a notch on anterior end, smooth and without enteric caeca or symbiont-containing structures ; tubular part with one enteric caecum on each side near its posterior end.

Hind gut S-shaped, broad at and behind posterior flexure, ending in a contracted tube leading to anus.

Six Malpighian tubules inserted anteriorly in three groups, two lateral groups of two long tubules, the other, dorsal, group of two short tubules ; applied in a group of three on each side of posterior flexure, each group of two long and one short tubule (see fig. 48).

Gymnetron antirrhini (Payk.)

Similar to *G. pascuorum* except that the proventriculus has the blade not concave anteriorly and the retaining bristles are about one-third the length of the blade.

Alcidodes fabricii Fab. (fig. 50)

Crop absent ; proventriculus (fig. 51) elongate and very weakly developed, blade consisting only of two rows of long bristles, becoming unpaired anteriorly ; some bristles on anterior part broad and serrated apically, posterior bristles pointed ; posterior oesophagus with short bristles ; cardiac valve without bristles.

Mid gut with distended part oblong, narrow anteriorly and broadened to posterior side, longer than broad and without enteric caeca or symbiont-containing structures ; tubular part bearing numerous enteric caeca all round behind middle.

Hind gut longer than tubular part of mid gut, narrow anteriorly, broadened behind posterior flexure and then abruptly constricted into a tube.

Six long Malpighian tubules inserted anteriorly in two groups of three tubules, one on each side ; applied at posterior flexure in a group of three on each side lateroventrally.

Cionus scrophulariae (L.) (fig. 52)

Crop absent ; proventriculus (fig. 53) well developed, without grinding plates ; blades not defined anteriorly and unpaired ; retaining bristles very short and pointed ; declivity teeth absent ; brushes of blade starting a little behind the anterior end and projecting into cardiac valve ; median without hairs ; blades not notched at intermedians, which project into oesophagus ; external intermedial fringe transversely striate ; posterior part of oesophagus with rows of long bristles in front of medians ; cardiac valve without bristles.

Mid gut with distended part ovoid, smooth and without enteric caeca or symbiont-containing structures ; tubular part with 3–5 long enteric caeca, very close to Malpighian tubules ; these caeca may be simple or bifurcate and arranged in two groups.

Hind gut longer than tubular part of mid gut, gradually broadened behind posterior flexure and then abruptly contracted into a tube.

Six long Malpighian tubules inserted all round mid gut, as stated by Stammer (1934) for the genus *Cionus* ; applied just behind posterior flexure in a group of three tubules on each side latero-ventrally.

Cionus sp.

Similar to *C. scrophulariae* except that the mid gut has 3–4 simple enteric caeca on the tubular part.

Anoplus plantaris (Naez.)

Crop absent ; proventriculus weakly developed (not examined in detail).

Mid gut with distended part narrow anteriorly and broadened posteriorly, without enteric caeca or symbiont-containing structures ; tubular part longer than distended part, with two rows of enteric caeca behind middle.

Hind gut tubular, gradually distended behind posterior flexure and then contracted, but posterior tube quite wide anteriorly.

Six Malpighian tubules (not examined in detail).

Rhynchaenus fagi (L.) (fig. 54)

Crop absent; proventriculus weakly developed, broader than oesophagus, without grinding plates; blade not defined and unpaired anteriorly; retaining bristles short and pointed; declivity teeth absent; bristles of blade short and on almost entire length; medians without hairs; blades not notched at intermedians; external intermedial fringe transversely striate and apparently serrated at the border; posterior part of oesophagus with scattered bristles; cardiac valve without bristles.

Mid gut with distended part ovoid, smooth and without enteric caeca or symbiont-containing structures; tubular part longer than ovoid part, with two rows each of 6–9 enteric caeca at about middle part at some distance from insertion of Malpighian tubules.

Hind gut distinctly shorter than mid gut; gradually broadened behind posterior flexure before being abruptly contracted into a tube leading to anus.

Six Malpighian tubules inserted anteriorly in a group of four long tubules on one side and two short ones inserted widely apart from each other; applied behind posterior flexure in a group of three on each side.

Rhynchaenus rusci (Hbst.)

Similar to *R. fagi* but tubular part of mid gut with 6–12 enteric caeca.

Rhamphus pulicarius (Hbst.) (fig. 55)

Oesophagus gradually broadened posteriorly; crop absent; proventriculus small, weakly developed and without grinding plates; blades unpaired and almost truncate anteriorly; retaining bristles fine and about half length of blade; declivity teeth absent; brushes of blade weak but present on entire length; declivities broad; medians not marked anteriorly and with neither hairs nor a posterior brush of projecting hair; blade not notched at intermedians; intermedial fringe serrated and present on entire length; posterior part of oesophagus and cardiac valve without bristles.

Mid gut with distended part ovoid, smooth and without enteric caeca or symbiont-containing structures; tubular part uniform in diameter, longer than distended part and having two rows each of 4–6 long enteric caeca at about middle of the tubular part.

Hind gut tubular, of almost uniform diameter except for abruptly distended posterior part, and with an abrupt contraction posterior to flexure.

Four Malpighian tubules of equal length inserted separately in one group anteriorly; applied behind posterior flexure in a group of two on each side.

Scolytus destructor Ol. (fig. 56)

Oesophagus short; crop well developed; proventriculus (fig. 57) strong and developed, with paired grinding plates notched on both sides of median, longer than blade, adjoining halves of plates rounded at intermedians anteriorly, with scaly structures which are longer and dense in two patches near medians; blades with long brushes, their bases forming small declivities; retaining bristles few in the hollow part; declivity teeth absent; blade touching only at one point at medians; grinding structures not notched at intermedians; external intermedial fringe present on entire length; crop and cardiac valve without bristles. Proventriculus agrees in general features with another species, *Scolytus* (*Eccoptogaster*) *scolytus* F., shown by Nüsslin (1911).

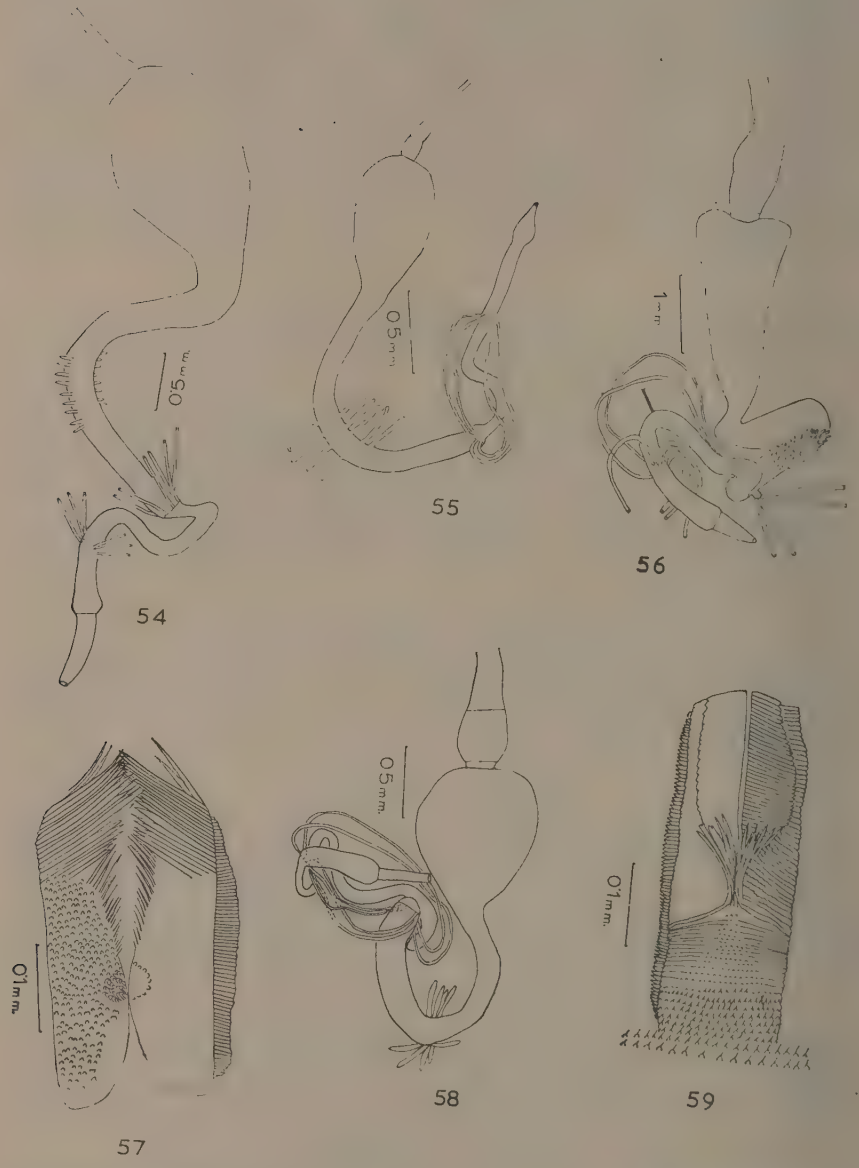
Mid gut with distended part emarginate anteriorly in male and with two nodules, possibly containing symbionts, in female, then gradually narrowed posteriorly and without enteric caeca; tubular part broad at about middle, narrowing to both ends, with a large number of enteric caeca all round gut behind middle and a little distance in front of insertion of Malpighian tubules.

Hind gut strongly coiled and gradually broadened behind posterior flexure, then contracted into a tube.

Six Malpighian tubules inserted anteriorly in two groups, one of four long tubules entering through a common chamber, the other of two short ones entering separately on other side; applied separately behind posterior flexure on lateral and ventral sides.

Hylastinus obscurus (Marsh.) (fig. 58)

Oesophagus short with a small crop; proventriculus (fig. 59) large and rounded on sides, with unpaired grinding plates having transverse lines followed by rows of tubercles, anterior



FIGS. 54–59.—(54–56) Alimentary canal of: (54) *Rhynchaenus fagi*; (55) *Rhamphus pulicarius*; (56) *Scolytus destructor*. (57) Proventricular blade of *S. destructor*. (58, 59) *Hylastinus obscurus*: (58) alimentary canal; (59) proventricular blade.

margin not defined except for a strong sclerotisation towards intermedians, between the sclerotisation continuous with the toothed intima of the crop ; blade longer than the unpaired plate and with declivities jointly notched anteriorly ; retaining bristles broad with apical spines, less than half length of blade ; declivity teeth in a number of rows, extending far posteriorly well into intermedians ; brushes present on entire length of blade and not serrated, medians only marked in the blade part and without hairs or a projecting posterior brush of hairs ; grinding structures not notched at intermedians ; external intermedial fringe formed by spines throughout ; crop with toothed intima but without bristles, cardiac valve without bristles.

Mid gut with distended part ovoidal, its surface impressed by the tubules and without enteric caeca or symbiont-containing structures ; tubular part of uniform diameter and with two bunches each of 3–5 long enteric caeca at about middle.

Hind gut coiled and pyriform behind posterior flexure.

Six Malpighian tubules inserted anteriorly in two groups, one of four long tubules, the other of two short ones, all tubules inserted separately ; applied behind posterior flexure in one group ventrally.

Phloeophthorus rhododactylus (Marsh.) (fig. 60)

Oesophagus short and broadened to form small crop ; proventriculus (fig. 61) well developed and rounded on sides, with unpaired grinding plates marked by homogeneous sclerotisation, almost truncate anteriorly and with curved, finely dentate lines ; blade longer than plate and declivities, almost straight anteriorly and posteriorly ; retaining bristles short, broad and toothed ; declivities with a row of teeth close to brushes and scattered teeth on side ; brushes of blade serrated internally, almost on entire length and not projecting into cardiac valve ; median without hairs or a posterior projecting brush of hairs and not marked throughout ; grinding structures not notched at intermedians and almost rectangular ; external intermedial fringe present thoughout ; crop with sclerotised intima, each scaly structure having a bluntly-pointed projection ; crop and cardiac valve without bristles.

Mid gut with distended part narrowed posteriorly, smooth and without enteric caeca or symbiont-containing structures ; tubular part not of uniform diameter, with 2–3 enteric caeca in one bunch on each side behind middle.

Hind gut tubular, coiled, broad behind posterior flexure, uniform up to anus but a muscular sheath, similar to that in *Sitophilus oryzae*, present near posterior end.

Six Malpighian tubules inserted separately in two groups, one of four long tubules, the other of two short ones ; applied at posterior flexure in one group ventrally.

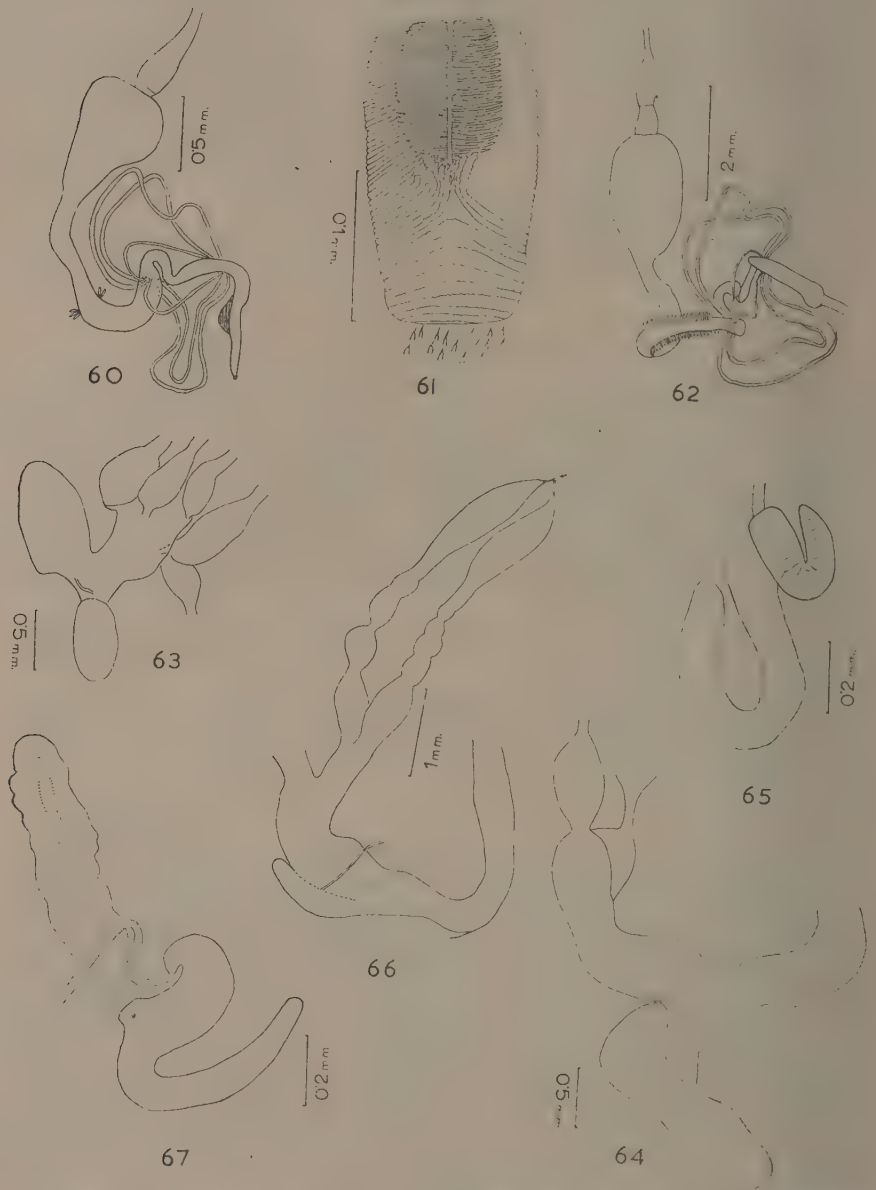
Myelophilus piniperda (L.) (fig. 62)

Oesophagus short, crop oblong and broader than proventriculus ; proventriculus (Nüsslin, 1911) well developed, with unpaired grinding plate demarcated from declivities of blade by two diverging rows of teeth (the cross lines of Nüsslin) towards intermedians, posterior teeth bigger and close to retaining bristles, rows of denticles running between cross lines and not clearly defined from the crop ; blade with declivities on both sides of unpaired plate, almost as long from retaining bristles onwards as the plate part, retaining bristles broad and reaching about half length of blade ; a few declivity teeth present near cross lines but teeth present externally on brushes ; brushes of blade not serrated internally, not projecting into cardiac valve and present on entire length of blade ; median not marked in the grinding plate and with neither hairs nor posterior brush of hairs projecting into cardiac valve ; grinding structures not incised at intermedians ; external intermedial fringe longer in middle and gradually shortened to both ends ; crop with transverse rows of denticles in front of each grinding structure and less developed in front of intermedians ; no bristles in crop or cardiac valve.

Mid gut with distended part ovoid, smooth and without enteric caeca or symbiont-containing structures ; tubular part longer than distended part, not of uniform diameter and with two rows each of 14–21 enteric caeca on posterior part, a little distance from posterior end.

Hind gut strongly coiled, gradually broadened behind posterior flexure, then abruptly contracted into a tube.

Six Malpighian tubules inserted separately in two groups, one of four long tubules, the other of two short ones ; applied behind posterior flexure in a group of three on each side, each group of one short and two long tubules.



Figs. 60–67.—(60, 61) *Phloeophthorus rhododactylus*: (60) alimentary canal; (61) proventricular blade. (62) Alimentary canal of *Myelophilus piniperda*. (63) Female reproductive organs of *Deporaus betulae*. (64, 65) *Apion miniatum*: (64) female reproductive organs; (65) spermatheca. (66, 67) *Otiorrhynchus singularis*: (66) female reproductive organs; (67) spermatheca.

Nüsslin (1911, 1912 and 1913) on numerous bark beetles, Russo (1937) on *Phloeotribus scarabaeoides* Bern., Kühn (1949) on *Ips typographus* L. and Maksymov (1950) on *I. curvidens* are works that have been taken into consideration but are too extensive to discuss here.

IV. The Female Reproductive System

The female reproductive system normally consists of the paired ovaries and lateral oviducts, the common oviduct, the vagina, the bursa copulatrix (sometimes absent), the spermatheca and, in some groups, the sclerotised posterior part of the vagina which forms the so-called ovipositor. Each laterally placed ovary has two acrotrophic ovarioles in the Curculionidae and Scolytidae but more than two in the Attelabidae. The size of the ovarioles depends on the maturity of the adults ; when mature the ovarioles contain well-developed egg rudiments.

Each ovariole may end in a terminal filament which unites with the filament from the other ovariole to form a short ligament. This joins the ligament from the other ovary to form a common median ligament, which runs posteriorly and becomes attached to the posterior flexure of the hind gut. Filaments and ligaments are absent in some species.

The ovarioles of each side open into the calyx of the lateral oviduct. The calyx varies in size according to the maturity of the female ; it is full of eggs in mature adults. The lateral oviducts unite to form the tubular common oviduct, which varies in length and broadens to form the vagina. The vagina may be either short, broad and almost ovoid, or long and almost cylindrical. The end of the common oviduct is clearly defined in species with a bursa copulatrix, but in those without one the vagina is recognisable mainly by its thicker, opaque walls, the common oviduct being translucent. The bursa copulatrix is either well developed, rudimentary or absent in Curculionidae *s.l.* The sclerotised terminal part of the vagina (the so-called ovipositor) is absent in most of the species studied. When present, it is either tubular or depressed and flat.

The spermatheca normally lies on the right-hand side of the system and is visible through the tergites. It varies greatly in shape and structure within the Curculionidae *s.l.* and consists of three main parts : the capsule, gland and duct. The capsule is curved and heavily sclerotised. It may have one or both dorsal arms (*i.e.* the collum and ramus of Spett and Lewitt, 1928) distinct and providing attachments for the duct and gland respectively, or both arms may be fused to form a thick basal part. The nodulus of the above authors is absent in the species studied except for *Ceuthorrhynchus pollinarius*. The cornu, or bent part of the capsule may be pointed or blunt apically. The spermathecal duct may be short and thick or very long, narrower and coiled. It always originates nearer the concave side of the capsule than does the gland and joins the main system at the common oviduct, or at the lower side or apex of the bursa copulatrix. The spermathecal gland is tubular, ovoid or subconical. It may enter the capsule directly in the middle or at the thick basal part, either directly or through a distinct ramus. The gland is usually filled with a white secretion. Spermathecal muscles are present in the concavity of the capsule.

The female reproductive organs of all the species studied are briefly described in the following pages.

Deporaus betulae (L.) (fig. 63)

Five short ovarioles in each ovary, three arising at a higher level than the other two, with filaments but without ligaments ; calyx very large in mature females, lateral oviducts short and constricted behind calyx ; common oviduct very short ; bursa copulatrix absent ; vagina with sides rounded and slightly narrowed posteriorly.

Spermatheca not seen.

Rozsypal (1939) studied the female reproductive organs in *Rhynchites pauxillus* Germ. and showed four ovarioles in each ovary ; large calyx : spermathecal duct short and entering the base of common oviduct ; gland elongate.

Apion miniatum Germ. (fig. 64)

Ovarioles with terminal filaments but without ligaments ; calyx absent ; lateral oviducts thicker than common oviduct ; bursa copulatrix very large, with broad, curved apex, longer than vagina but oval in mature females ; vagina almost as long as broad, posterior sclerotised tubular part absent.

Spermatheca (fig. 65) with capsule not reticulate, strongly curved ; tip blunt, gradually broadened to basal part ; without collum and ramus, rounded basally ; duct and gland entering very close to each other, duct short and thick, gland long and tubular.

Apion ulicis (Forst.)

Similar to that of *A. miniatum* and agrees with the description of female reproductive organs of this species by Davies (1928) but vagina continued as a narrowed and non-sclerotised tube posteriorly, supported laterally by two sclerotised bars ; spermatheca having capsule with some reticulations and transverse depressed lines ; duct and ovoid, stalked gland entering broad anterior part internally.

Apion radiolus Kirby

Similar to *A. miniatum* but common oviduct thicker than lateral oviducts and vagina with broad non-sclerotised tube posteriorly supported by two sclerotised lateral bars.

Spermatheca not seen.

Apion immune Kirby

Generally similar to *A. radiolus* but the spermatheca resembles *A. ulicis*, except that the gland and duct enter on the externo-apical side.

The female reproductive organs in *Piezotrachelus varium* Wag. and *Apion chirindanum* Wag. are similar to those of *A. miniatum* and are described by Phelps (1956).

Otiorrhynchus singularis (L.) (fig. 66)

Ovarioles with terminal filaments and ligaments ; distinct calyx absent ; lateral oviduct only slightly broadened to apex and short ; common oviduct longer than lateral ones and also broader than either vagina or bursa copulatrix ; bursa copulatrix narrow and finger-shaped ; vagina tubular, broader anteriorly, elongate and narrow posteriorly, posterior part strongly sclerotised.

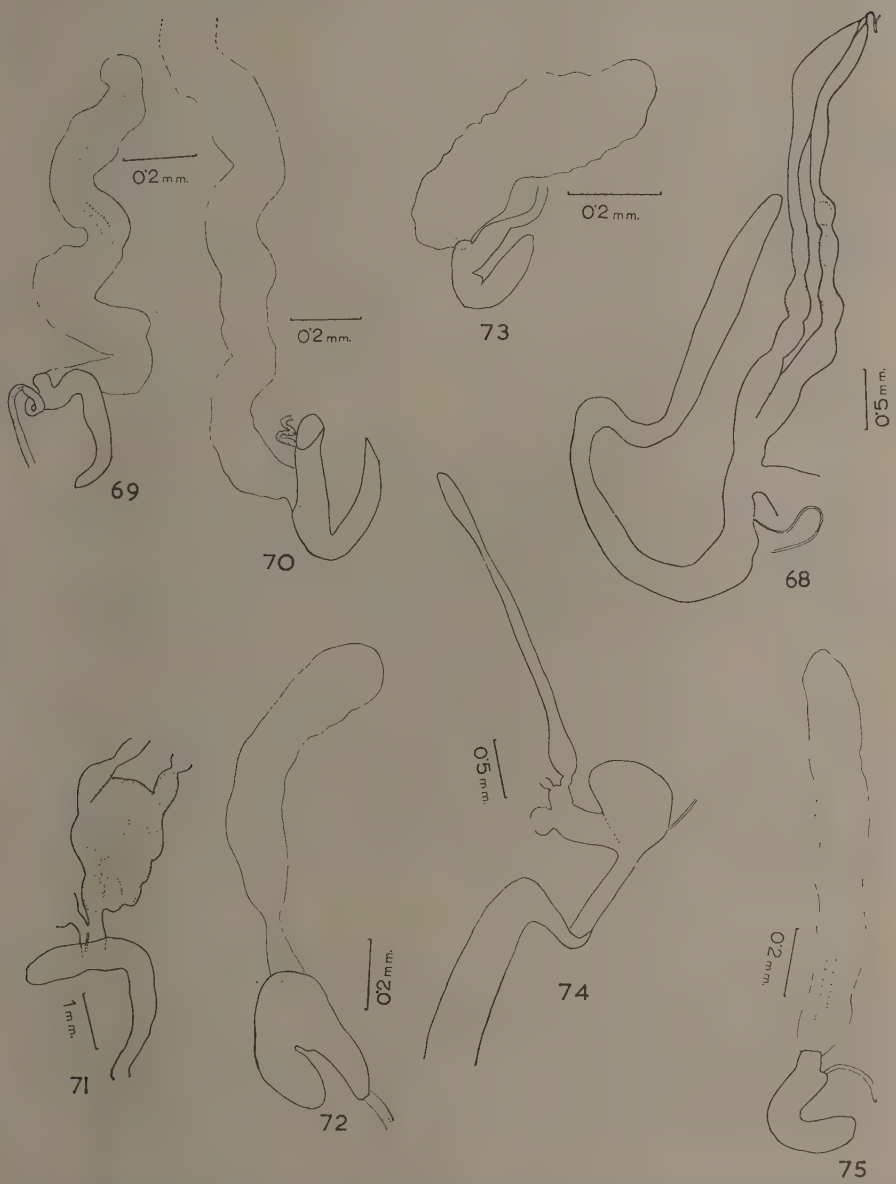
Spermatheca (fig. 67) with capsule strongly but not uniformly sclerotised, broad basally and narrow apically ; collum reticulate, well developed and curved ; ramus small and arising on outer side of capsule ; spermathecal duct very long, coiled, leaving the bent tip of collum and entering bursa copulatrix on its under side ; gland almost tubular, with irregular outline, entering ramus through the invaginated funnel.

The female reproductive organs in *Naupactus leucoloma* Boh. (Tissot, 1938) are similar to those of *O. singularis* except that the spermathecal duct enters the common oviduct and the gland is tubular.

Myllocerus sp. nov. (fig. 68)

Ovarioles long with filaments and ligaments ; distinct calyx absent ; lateral oviducts short and broad towards ovarioles and narrow posteriorly ; common oviduct longer but narrower than lateral oviduct ; bursa copulatrix small and closely applied to the vagina ; vagina long, tubular, S-shaped and narrowed posteriorly, posterior part sclerotised.

Spermatheca (fig. 69) with capsule not uniformly sclerotised, slightly broad basally and bluntly narrowed to apex ; collum projecting, looped over itself and faintly reticulate ; ramus distinct and broad apically ; spermathecal duct long, narrow, leaving tip of collum and entering common oviduct dorso-laterally on right-hand ; gland long, tubular, entering ramus through an invaginated funnel.



FIGS. 68–75.—(68, 69) *Myllocerus* sp. nov. : (68) female reproductive organs ; (69) spermatheca. (70) Spermatheca of *M. maculosus*. (71, 72) *Phyllobius pyri* : (71) female reproductive organs ; (72) spermatheca. (73) Spermatheca of *P. virideaeris*. (74, 75) *Polydrosus tereticollis* : (74) female reproductive organs ; (75) spermatheca.

Myllocerus maculosus Desb.

Agrees with the preceding species but spermatheca (fig. 70) with capsule more pointed apically; long collum bent over itself, broad and not reticulate; ramus hardly distinct; gland longer and entering capsule through a funnel-shaped invagination.

Phyllobius pyri (L.) (fig. 71)

Ovarioles with terminal filaments and ligaments; calyx present; lateral oviducts short and narrower than common oviduct; common oviduct narrower than vagina; bursa copulatrix well developed and projecting; vagina tubular, long and broad anteriorly, narrow and sclerotised posteriorly.

Spermatheca (fig. 72) with capsule pigmented, strongly curved but not uniformly sclerotised; collum reticulate and narrower than tip of capsule; ramus absent; spermathecal duct short, leaving collum and entering bursa copulatrix on underside near base; gland tubular, with a basal stalk, entering bend of capsule externally through an invaginated funnel.

Phyllobius virideaeris (Laich.)

Agrees with *P. pyri* but spermatheca (fig. 73) with capsule unpigmented; ramus short; spermathecal duct enters common oviduct under bursa copulatrix; gland tubular but without a stalk, entering capsule towards collum.

Polydrosus tereticollis (DeGeer) (fig. 74)

Ovarioles long, with filaments and ligaments; calyx present; lateral oviducts short; common oviduct narrow posteriorly and longer than lateral oviducts; bursa copulatrix large, oval and much broader than common oviduct; vagina tubular, long, broader and sclerotised posteriorly.

Spermatheca (fig. 75) with capsule not uniformly sclerotised; collum short; ramus developed, projecting in front of collum and truncate at apex; collum, ramus and anterior part of capsule reticulate; spermathecal duct long, entering bursa copulatrix dorsally; gland tubular, entering ramus through an invaginated funnel.

Strophosomus melanogrammus (Forst.) (fig. 76)

Ovarioles as in *P. tereticollis*; calyx large; lateral oviducts shorter than common oviduct; common oviduct narrow at its junction with bursa copulatrix; bursa copulatrix well developed and sclerotised dorsally; vagina long, tubular, narrowed and sclerotised posteriorly.

Spermatheca (fig. 77) with capsule uniformly sclerotised, acutely bent and hexagonally reticulate except for a triangular apical area which is longitudinally reticulate; collum projecting in front of apex of capsule; ramus absent; spermathecal duct short, entering bursa copulatrix ventrally at its junction with common oviduct; gland long, tubular, entering externally in the middle of capsules through an invaginated funnel.

Parisomias sp. nov. (fig. 78)

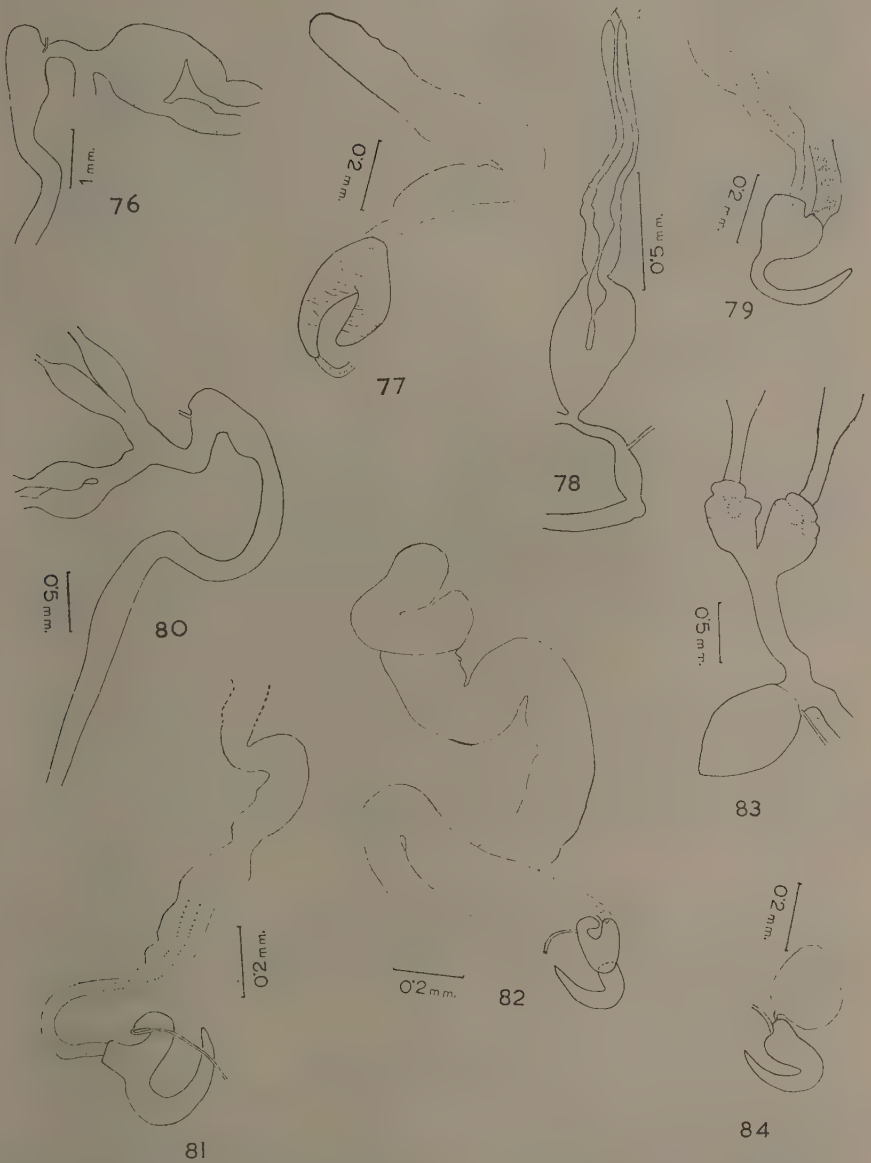
Ovarioles long with filaments and ligaments, base of each ovariole enlarged to form a chamber continuous with large calyx; lateral oviduct short; common oviduct narrow and long; bursa copulatrix absent; vagina tubular, straight and narrow, sclerotised posteriorly.

Spermatheca (fig. 79) not reticulate, capsule with more strongly sclerotised bulbus (anterior part) and a narrow posterior hook; collum and ramus distinct, former narrower than latter and almost truncate; spermathecal duct long, strongly coiled, arising from apex of collum and entering common oviduct dorsally; gland tubular, broader apically and stalked basally.

Amblyrrhinus subrecticollis Marsh. (fig. 80)

Ovarioles with terminal filaments and ligaments; calyx absent; lateral oviducts short; common oviduct longer than lateral oviduct; bursa copulatrix small and rudimentary; vagina with short broad anterior part and a long tubular posterior part which is sclerotised behind.

Spermatheca (fig. 81) with capsule uniformly sclerotised, broader at base and pointed apically; collum narrow, curved and reticulate; ramus broad and truncate apically, smooth as is the rest of the capsule; spermathecal duct long, narrow, entering common oviduct dorsally; gland coiled, very long, tubular, longer than the duct.



FIGS. 76–84.—(76, 77) *Strophosomus melanogrammus*: (76) female reproductive organs; (77) spermatheca. (78, 79) *Parisomias* sp. nov.: (78) female reproductive organs; (79) spermatheca. (80, 81) *Amblyrrhinus subrecticollis*: (80) female reproductive organs; (81) spermatheca. (82) Spermatheca of *Amblyrrhinus* sp. nov. (83, 84) *Sitona regensteinensis*: (83) female reproductive organs; (84) spermatheca.

Amblyrrhinus sp. nov.

Agrees with *A. subrecticollis* except that the spermatheca has a thick wall and a distinct bulbus (fig. 82).

Sitona regensteinensis (Hbst.) (fig. 83)

Ovarioles with filaments and ligaments ; base of each ovariole sometimes enlarged (as in the specimen figured) but not so in others ; nodule-like structures present ; calyx absent ; lateral oviducts much longer than common oviduct ; common oviduct broader than long ; bursa copulatrix absent ; vagina short, stout, ovoid and without sclerotised tubular part.

Spermatheca (fig. 84) with capsule more sclerotised than the pointed apex and not reticulate ; collum not distinct ; ramus short, rounded ; spermathecal duct long, leaving base of ramus and entering the common oviduct dorsally ; spermathecal gland small, ovoid, stalked, entering ramus through an invaginated funnel.

Sitona sp.

Agrees with *S. regensteinensis* except that the spermatheca has a less differentiated ramus.

Hypolixus truncatulus (Fab.) (fig. 85)

Ovarioles with terminal filaments and ligaments ; calyx large ; lateral oviducts behind calyx shorter than tubular common oviduct ; bursa copulatrix very small ; vagina ovoidal and short, sclerotised tubular part absent ; one symbiont-containing structure present on each side of vagina, opening on membrane between eighth and ninth sterna.

Spermatheca (fig. 86) with capsule reticulate and broad anteriorly, pointed and smooth apically; collum and ramus not differentiated ; spermathecal duct short, entering common oviduct dorsally on right side ; vesiculate gland ovoid, pointed apically, entering capsule through an invagination at same level as duct.

Conorhynchus brevirostris Gyll.

Agrees with *Hypolixus* but calyx absent (probably because of the immaturity of the females dissected).

Spermatheca (fig. 87) with capsule strongly sclerotised externally and apically, smooth except for reticulated collum and ramus ; collum thick ; ramus truncate at apex and lying at right angles to collum ; spermathecal duct very short and entering common oviduct dorsally ; gland large, vesiculate, ovoid, entering capsule through a tubular invagination.

Xanthochelus faunus Ol.

Agrees with *Conorhynchus* but spermatheca (fig. 88) with capsule more strongly sclerotised anteriorly, smooth and gradually narrowed to apex ; collum long and narrowed apically ; ramus well developed ; spermathecal duct short, entering common oviduct dorsally ; gland large, ovoid, vesiculate, entering the ramus through a tube-like invagination.

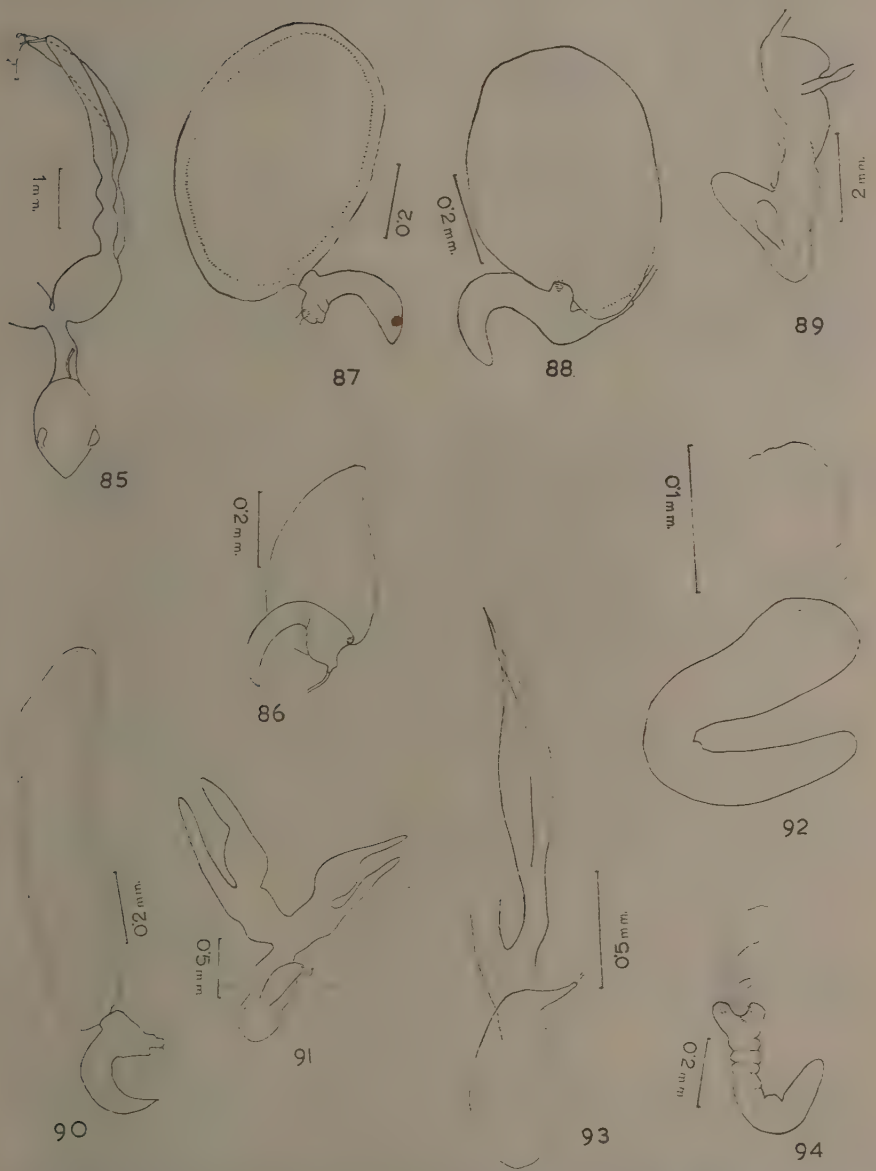
Neocleonus sanio Hbst. (fig. 89)

Similar to *Hypolixus* but symbiont-containing structures club-shaped, as in *Conorhynchus*, and bursa copulatrix large.

Spermatheca (fig. 90) with capsule pointed apically and smooth behind, projecting reticulate collum and ramus ; spermathecal duct short, entering common oviduct ; gland tubular, vesiculate, entering ramus though a tube-like invagination.

Pentarthrum huttoni Woll. (fig. 91)

Ovarioles short, without terminal filaments and ligament ; lateral oviduct broad, forming calyx ; bursa copulatrix well-developed and finger-shaped ; vagina ovoid, without sclerotised posterior tube.



FIGS. 85–94.—(85, 86) *Hypolixus truncatulus*: (85) female reproductive organs; (86) spermatheca. (87, 88) Spermatheca of (87) *Conorhynchus brevirostris*: (88) *Xanthochelus faunus*. (89, 90) *Neocleonus sanio*: (89) female reproductive organs; (90) spermatheca. (91, 92) *Pentarthrum huttoni*: (91) female reproductive organs; (92) spermatheca. (93, 94) *Dorytomus tortrix*: (93) female reproductive organs; (94) spermatheca.

Spermatheca (fig. 92) broadened at base, without collum and ramus; spermathecal duct short, leaving capsule through a tube and entering bursa copulatrix at apex, gland ovoid with irregular outline, stalked basally, entering capsule through an invaginated funnel.

Chararas (1956) has shown one ovariole in each ovary in *Rhyncolus porcatus* Germ., but two lying free in haemocoele in *R. elongatus* Gyll., *Pentarthrum huttoni* and *Caulotrupis aeneopiceus* Boh.

Dorytomus tortrix (L.) (fig. 93)

Ovarioles with terminal filaments and ligaments; lateral oviducts narrow; calyx absent; common oviduct broader than lateral oviducts; bursa copulatrix well developed, narrowed apically; outline of vagina oval *in situ* but appearing prolonged when genital segments are pulled out, without sclerotised tube.

Spermatheca (fig. 94) with capsule uniformly sclerotised and not reticulate; collum and ramus differentiated as the anterior bifurcation of the capsule; spermathecal duct short, thick, leaving outer incurved side of collum from an invaginated tube and entering narrowed apex of bursa copulatrix; gland elongate, thickened towards apex and entering ramus through an invaginated funnel.

Dorytomus rufatus (Bed.)

Similar to *D. tortrix* but calyx present; common oviduct not broader than lateral oviduct, bursa copulatrix absent. Spermatheca (fig. 95) with capsule differently shaped, more strongly sclerotised and reticulate; collum projecting in front of ramus; spermathecal duct entering common oviduct; gland broader and somewhat elongate.

Dorytomus dejeani (Fst.)

Similar to *D. tortrix* but bursa copulatrix more developed and apically rounded; vagina long, when fully extended; spermatheca with capsule reticulate; spermathecal duct entering dorsal right-hand side of bursa copulatrix; gland of uniform diameter.

Miccotrogus picirostris (Fab.) (fig. 96)

Ovarioles long, with terminal filaments but without ligaments; without distinct calyx; lateral oviducts shorter than common oviduct; bursa copulatrix well developed; vagina oblong but without sclerotised tubular part.

Spermatheca (fig. 97) with capsule smooth, not uniformly sclerotised, broadest near apex; collum small, arising from inner side of capsule; ramus stout and rounded apically; spermathecal duct short, narrow, entering common oviduct dorsally at its juction with bursa; gland almost spherical, entering ramus through an invaginated funnel.

Sibinia arenariae Steph.

Similar to *Miccotrogus* but ovarioles shorter; common oviduct much broader and longer than lateral ones; vagina short, tubular and without long sclerotised part.

Spermatheca not seen.

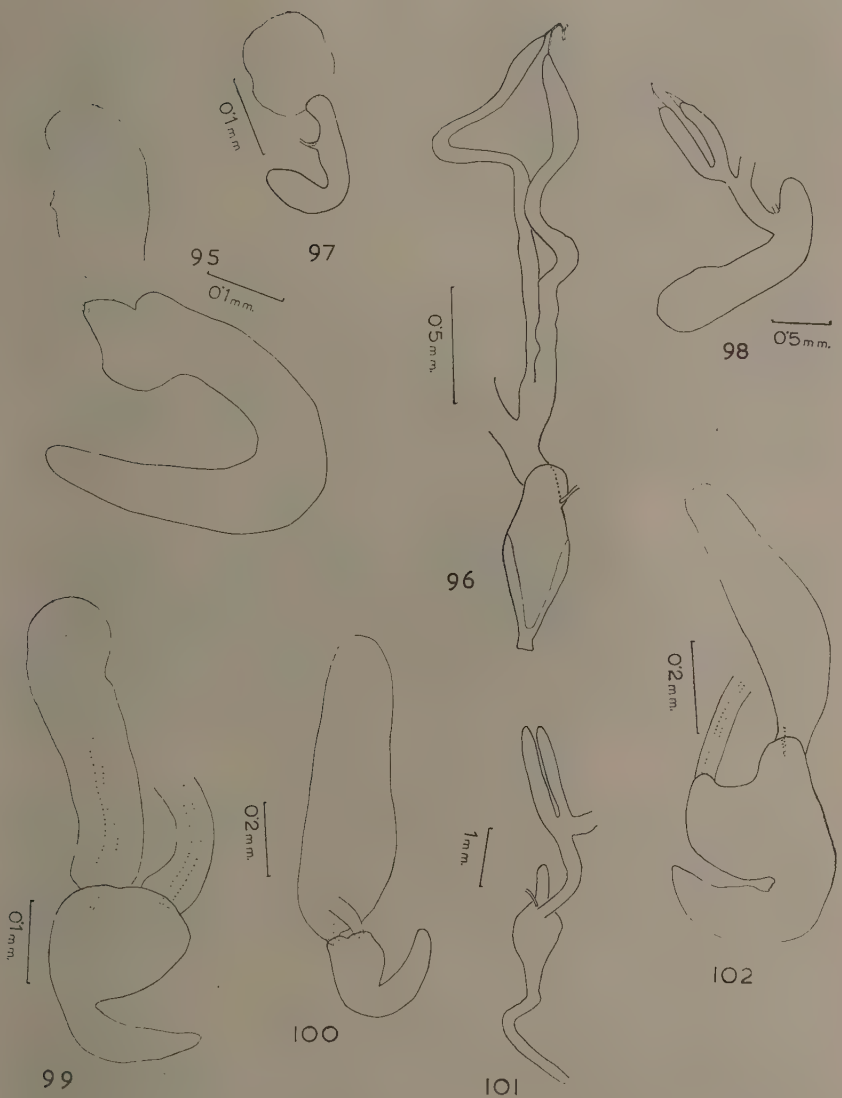
Anthonomus pedicularius (L.) (fig. 98)

Ovarioles with terminal filaments and ligaments; calyx not distinct; lateral oviducts short and broad; common oviduct long and tubular; bursa copulatrix large and projecting; vagina tubular, long, broad posteriorly but without sclerotised posterior tube.

Spermatheca (fig. 99) with capsule smooth, a large bulbus anteriorly, narrowed behind curve; differentiated collum and ramus absent; spermathecal duct short, entering common oviduct dorsally at its junction with bursa; gland long, tubular, entering bulbus through an invaginated funnel.

Anthonomus inversus Bed.

Similar to *A. pedicularius* except that the lateral oviducts are longer, the common oviduct lies ventral to the vagina, the bursa copulatrix is rudimentary and not projecting, and the vagina is tubular, longer than broad.



FIGS. 95–102.—(95) Spermatheca of *Dorytomus rufatus*. (96, 97) *Miccotrogus picirostris*: (96) female reproductive organs; (97) spermatheca. (98, 99) *Anthonomus pedicularius*: (98) female reproductive organs; (99) spermatheca. (100) Spermatheca of *Balaninus glandium*. (101–102) *B. venosus*: (101) female reproductive organs; (102) spermatheca.

Anthonomus pomorum (Miles, 1923 ; Vukasovic, 1932) and *A. cinctus* (Vukasovic, 1932) have similar female reproductive systems (including spermatheca).

Balaninus glandium (Marsh.)

Ovarioles with terminal filaments and ligaments ; without distinct calyx ; lateral oviducts shorter than common oviduct ; bursa copulatrix tubular, finger-like ; vagina coiled, tubular, broad anteriorly, narrowed and sclerotised posteriorly.

Spermatheca (fig. 100) with capsule smooth, base broad, blunt and narrow at apex ; collum hardly differentiated, ramus slightly projecting ; spermathecal duct short, entering the system at junction of bursa and common oviduct dorsally ; gland vesiculate, elongate-ovoid, longer than duct, entering ramus through an invaginated funnel.

Balaninus venosus Grav. (fig. 101)

Similar to *B. glandium* but vagina much broader and more rounded than in above species. Spermatheca (fig. 102) with capsule having differentiated collum and ramus ; spermathecal duct slightly shorter than gland, entering base of bursa copulatrix on underside.

The female reproductive organs in *Curculio caryae* Horn (Bissel, 1937) are similar to *B. glandium* except that the spermathecal duct is moderately long and enters the vagina at its anterior end.

Balanobius pyrrhoceras Marsh. (fig. 103)

Ovarioles with filaments but without ligaments ; whole of lateral oviduct enlarges to form calyx, longer than short and tubular common oviduct ; bursa copulatrix well developed and projecting ; vagina curved, long, tubular, narrowed and sclerotised posteriorly.

Spermatheca (fig. 104) with smooth, strongly sclerotised capsule having irregular lines on both sides of anterior bulbus ; collum and ramus short, stout and broad at apex ; spermathecal duct short, leaving collum through an invaginated tube and entering common oviduct on its right dorsal side ; gland ovoid or oblong, vesiculate, entering ramus through an invaginated funnel.

Hylobius abietis (L.) (fig. 105)

Ovarioles with filaments and ligaments ; lateral oviduct broadened to form calyx ; common oviduct short and tubular ; bursa copulatrix well developed and projecting ; vagina narrow anteriorly, broad and rounded posteriorly, sclerotised tubular part absent.

Spermatheca (fig. 106) with capsule unevenly sclerotised, smooth except for collum ; collum reticulate, broad at base and narrowed apically ; ramus well developed, truncate at apex, lying almost at right angles to collum ; spermathecal duct very short, entering bursa on its ventral side; gland elongate or elongate-ovoid, vesiculate, entering ramus through an invaginated funnel.

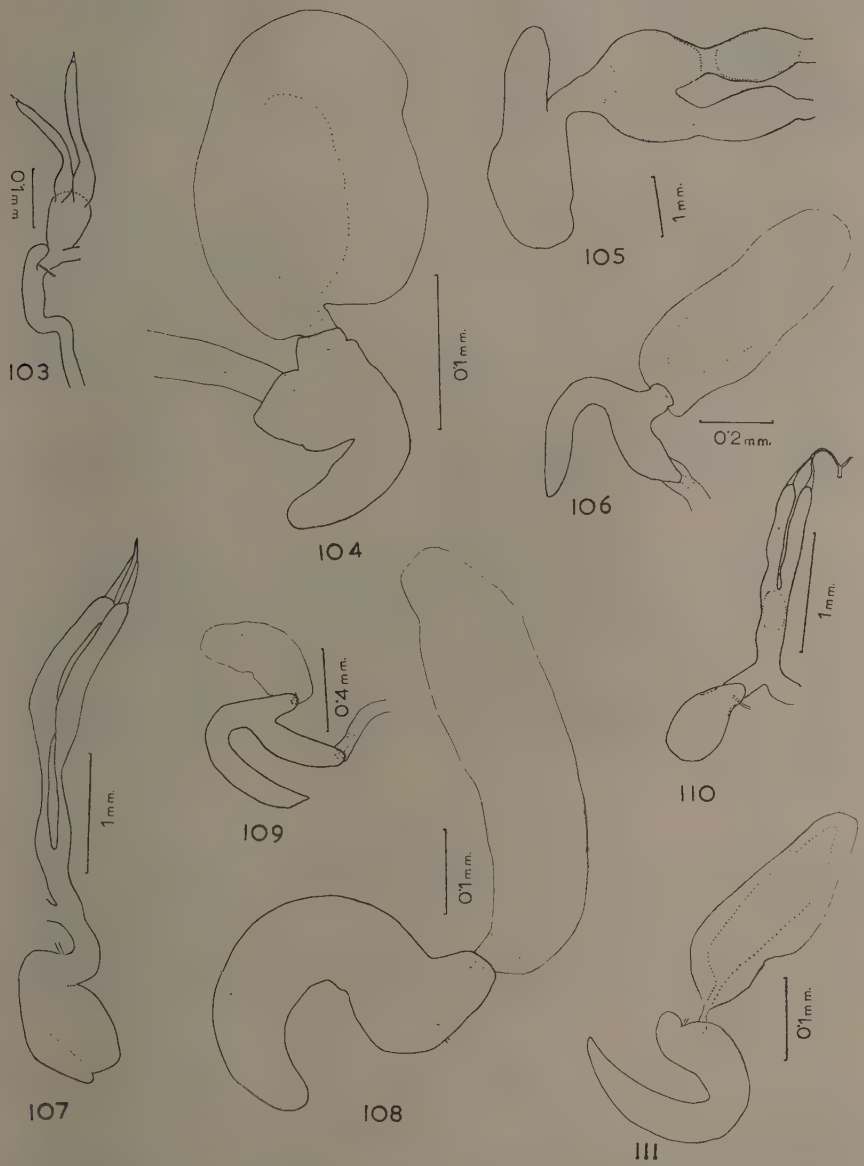
Hypera murina (Fab.) (fig. 107)

Ovarioles with terminal filaments and ligaments ; calyx absent ; lateral oviducts shorter than common oviduct, which runs dorsad posteriorly ; bursa copulatrix absent ; vagina broad, stout, without sclerotised tubular part.

Spermatheca (fig. 108) with capsule not uniformly sclerotised, reticulate throughout, blunt apically ; collum not differentiated ; ramus projecting, rounded apically ; spermathecal duct short, leaving capsule through a tube and entering common oviduct on dorsal left at its junction with vagina ; gland broad, tubular, not vesiculate.

Hypera punctata (Fab.)

Similar to *H. murina* but calyx large and longer than common oviduct. Spermatheca (fig. 109) with differently shaped capsule, smooth and uniformly sclerotised ; collum and ramus well differentiated, former longer than latter.



FIGS. 103–111.—(103, 104) *Balanobius pyrrhoceras*: (103) female reproductive organs; (104) spermatheca. (105, 106) *Hylobius abietis*: (105) female reproductive organs; (106) spermatheca. (107, 108) *Hypera murina*: (107) female reproductive organs; (108) spermatheca. (109) Spermatheca of *H. punctata*. (110, 111) *Gronops lunatus*: (110) female reproductive organs; (111) spermatheca.

Gronops lunatus (Fab.) (fig. 110)

Ovarioles with terminal filaments and ligaments ; calyx absent ; lateral oviducts broader than common oviduct, both being fairly long ; bursa copulatrix well developed and projecting ; vagina short, broad, without sclerotised tubular part.

Spermatheca (fig. 111) with capsule not uniformly sclerotised, smooth externally, broad at base and pointed at tip ; collum produced ; ramus not differentiated ; spermathecal duct short, leaving capsule at one side near junction of latter with collum and entering common oviduct at its junction with bursa ; gland long, leaf-shaped, entering capsule through an invaginated funnel.

Sitophilus oryzae (L.)

Ovarioles stout and with short terminal filaments, without ligaments ; lateral oviducts short, without distinct calyx ; common oviduct running dorsad posteriorly ; bursa copulatrix with very short projecting part closely applied to common oviduct ; vagina elongate, without sclerotised tubular part.

Spermatheca (fig. 112) with capsule reticulate, unevenly sclerotised, bluntly pointed apically, slightly broader at base ; collum and ramus hardly differentiated ; spermathecal duct moderately long, leaving capsule through an invaginated tube and entering vagina dorsally ; gland small with irregular outline, entering capsule though an invaginated funnel.

Calandra oryzae (Müller, 1928 ; Murray and Tiegs, 1935 ; Traiman, 1937) and *C. granaria* (Müller, 1928 ; Krautwig, 1930 ; Andersen, 1938) have been studied for the female reproductive organs.

Cosmopolites sordidus Aur. (fig. 113)

Ovarioles with terminal filments and without ligaments ; lateral oviducts enlarged to form calyx ; common oviduct short, bursa copulatrix defined but closely attached to common oviduct ; vagina broader than bursa, longer than broad, without tubular sclerotised posterior part.

Spermatheca (fig. 114) with capsule not uniformly sclerotised, not reticulate, pointed apically and broad anteriorly ; collum projecting in front of small indistinct ramus, which is represented only by a notch in the capsule ; spermathecal duct moderately long, entering collum through an invaginated tube (entry into the system not seen), gland tubular, entering capsule through an invaginated funnel.

Coeliodes rubicundus (Hbst.) (fig. 115)

Ovarioles with terminal filaments and ligaments ; calyx not marked ; lateral oviducts broad and shorter than common oviduct ; bursa copulatrix projecting ; vagina stout, somewhat longer than broad and without a tubular sclerotised part.

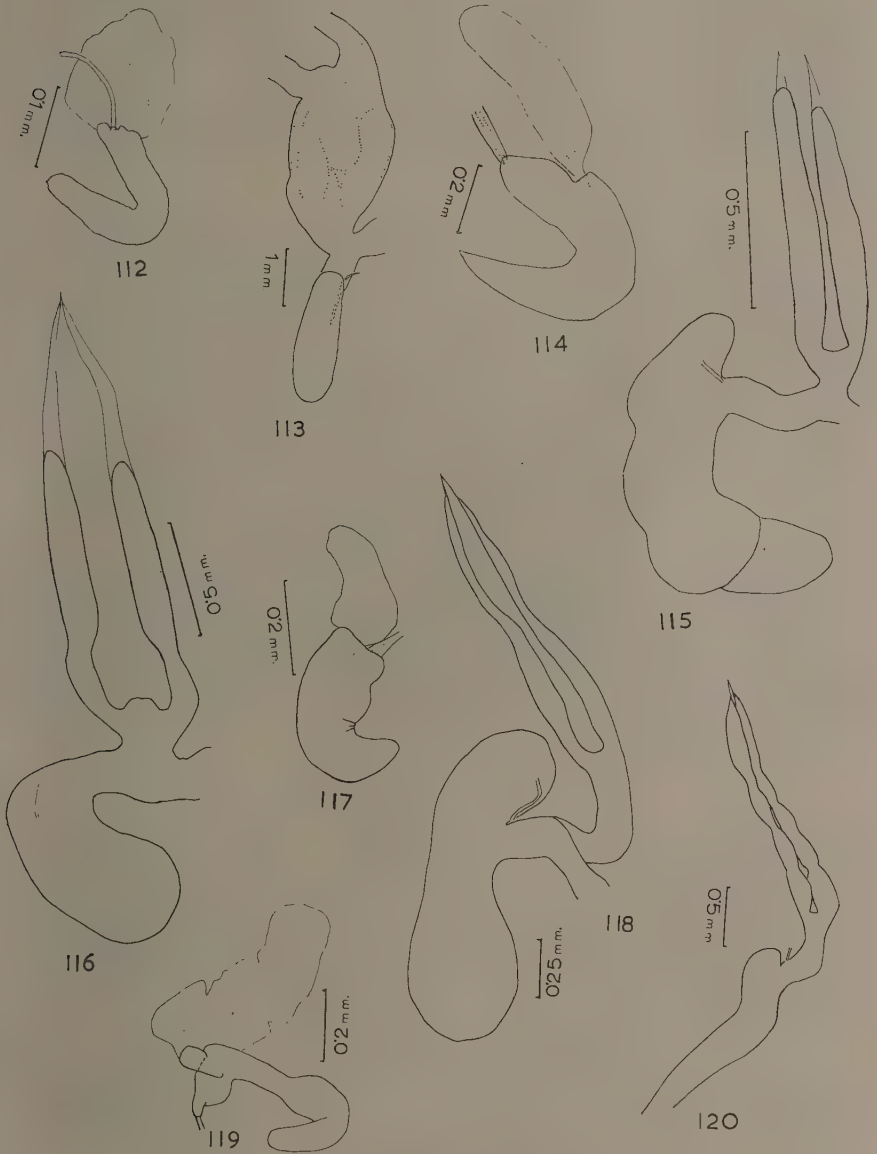
Spermatheca with capsule more sclerotised externally, broad and reticulate anteriorly, smooth and blunt to apex ; collum and ramus not differentiated ; spermathecal duct short, leaving capsule through an invaginated tube and entering common oviduct at its junction with bursa copulatrix ; gland tubular with irregular outline, entering capsule through an invaginated funnel.

Micrelus ericae (Gyll.)

Ovarioles with filaments and without ligaments ; lateral oviduct broadened to form calyx ; common oviduct short ; bursa copulatrix large, projecting ; vagina tubular, not strongly sclerotised.

Spermatheca with capsule not reticulate, almost uniformly sclerotised, of almost uniform diameter on each side of bend ; collum rounded and thick ; ramus undifferentiated ; duct and gland both enter capsule externally ; spermathecal duct short, entering capsule through an invaginated funnel (entry into the system not seen) ; gland tubular with irregular outline, entering capsule through an invaginated funnel.

Stenocarus fuliginosus (Rozsypal, 1941) is as above except that the ovarioles are with ligaments and the spermathecal duct enters the common oviduct laterally.



FIGS. 112–120.—(112) Spermatheca of *Sitophilus oryzae*. (113, 114) *Cosmopolites sordidus*: (113) female reproductive organs; (114) spermatheca. (115) Female reproductive organs of *Coeliodes rubicundus*. (116, 117) *Cidnorrhinus quadrimaculatus*: (116) female reproductive organs; (117) spermatheca. (118, 119) *Ceuthorrhynchus pollinarius*: (118) female reproductive organs; (119) spermatheca. (120) Female reproductive organs of *Rhinoncus pericarpius*.

Cidnorrhinus quadrimaculatus (L.) (fig. 116)

Ovarioles with filaments and ligaments ; lateral oviducts short and broad ; common oviduct longer than lateral ones ; bursa copulatrix absent ; vagina tubular, though appearing rounded at sides *in situ* because the ventrally recurved tubular part lies beneath the remainder. (In one specimen three ovarioles on one side and two on the other.)

Spermatheca (fig. 117) with capsule more sclerotised externally, reticulate towards base and smooth towards blunt apex ; collum and ramus not differentiated ; spermathecal duct short, entering common oviduct on dorso-lateral side and leaving capsule through an invaginated tube ; gland longer than broad, tapering to apex and entering the capsule through an invaginated funnel.

Ceuthorrhynchus pollinarius Forst. (fig. 118)

Ovarioles similar to *Cidnorrhinus* ; lateral oviducts long with numerous small nodules on calyx ; common oviduct shorter than lateral oviduct ; bursa copulatrix large, projecting ; vagina broad anteriorly, with a short posterior tube recurved beneath anterior part *in situ*.

Spermatheca (fig. 119) with capsule uniformly sclerotised ; collum and ramus distinct and at right angles to each other ; narrowed anteriorly, blunt apically, reticulate between collum and bend, rest smooth ; spermathecal duct as long as capsule, arising from tube of collum and entering bursa copulatrix on right-ventral side ; gland with irregular outline, entering truncated ramus through an invagination.

Gunthart (1949) has shown similar female reproductive organs in *C. quadridens* and *napi*.

Rhinoncus pericarpius (L.) (fig. 120)

Ovarioles with neither terminal filaments nor ligaments ; calyx present, not differentiated in immature females ; lateral oviducts longer than common oviduct ; bursa copulatrix small but distinct ; vagina tubular with a short, sclerotised posterior part.

Spermatheca (fig. 121) with capsule pointed apically, almost uniformly sclerotised and smooth ; collum broad and rounded apically ; ramus separated from collum by a notch, its outline continuous with the posterior part of capsule ; spermathecal duct short, leaving collum through an invaginated tube and entering bursa copulatrix on right-ventral side ; gland short, tubular, entering capsule through an invaginated funnel.

Gymnetron pascuorum (Gyll.) (fig. 122)

Ovarioles with terminal filaments but without ligaments ; lateral oviducts long, broader at their junction, without calyx ; common oviduct long, tubular ; bursa copulatrix absent ; vagina oval in outline, short and without sclerotised posterior tube.

Spermatheca (fig. 123) on left side of vagina ; capsule more sclerotised externally, not reticulate, with an anterior bulbus and a posterior narrow blunt hook ; collum and ramus not differentiated ; spermathecal duct longer than capsule, leaving bulbus by an invaginated tube and entering junction of common oviduct and vagina ; gland short, vesiculate, entering bulbus through an invaginated funnel.

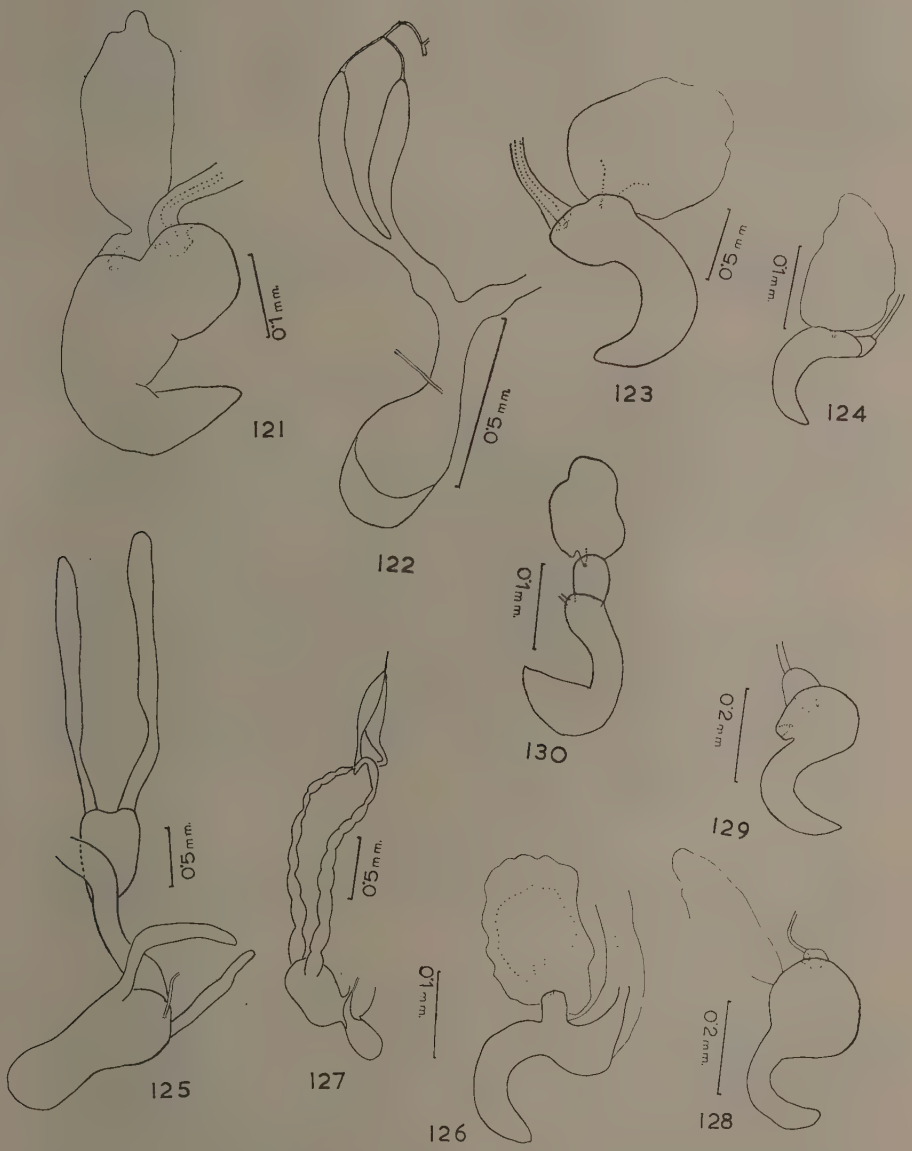
Gymnetron antirrhini (Payk.)

Similar to *G. pascuorum* except in the spermatheca (fig. 124), which differs in shape.

Alcidodes fabricii Fab. (fig. 125)

Ovarioles with terminal filaments and ligaments ; lateral oviducts tubular or enlarged anteriorly into calyx ; common oviduct long ; bursa copulatrix rudimentary ; vagina short, with genitalia sole-shaped in outline, bearing one long, transparent and tubular symbiont-containing structure on either antero-lateral side, without posterior sclerotised tube.

Spermatheca (fig. 126) with capsule strongly but not uniformly sclerotised, broadly arched and reticulate ; collum narrow and tubular ; ramus projecting, abruptly contracted into a tube ; spermathecal duct short, leaving tubular collum and entering junction of common oviduct and bursa copulatrix ; gland vesiculate, ovoid, entering ramus through an invaginated tube.



FIGS. 121–130.—(121) Spermatheca of *Rhinoncus pericarpius*. (122, 123) *Gymnetron pascuorum*: (122) female reproductive organs; (123) spermatheca. (124) Spermatheca of *G. antirrhini*. (125, 126) *Alcidodes fabricii*: (125) female reproductive organs; (126) spermatheca. (127, 128) *Cionus scrophulariae*: (127) female reproductive organs; (128) spermatheca. (129, 130) Spermatheca of: (129) *Cionus* sp.; (130) *Anoplus plantaris*.

Cionus scrophulariae (L.) (fig. 127)

Ovarioles very long, with terminal filaments and ligaments ; lateral oviducts enlarged to form calyx ; common oviduct short ; bursa copulatrix absent ; vagina with rounded sides, longer than common oviduct, without posterior sclerotised tubular part.

Spermatheca (fig. 128) with capsule smooth, not uniformly sclerotised, with a large anterior bulbus and narrowed hook ; collum and ramus undifferentiated ; spermathecal duct very long, coiled, enlarged at base before its entry at junction of common oviduct and vagina, leaving bulbus apically through a strong, broad, invaginated tube ; gland ovoid, small, entering bulbus through an invaginated funnel.

Cionus sp.

Similar to *C. scrophulariae* but spermatheca (fig. 129) with smaller bulbus ; spermathecal duct leaving bulbus subapically and not enlarged before entering junction of common oviduct and vagina ; gland entering junction of bulbus and hook of capsule externally.

Anoplus plantaris (Naez.)

Ovarioles with terminal filaments and ligaments ; lateral oviducts long and broadened apically to form calyx ; common oviduct broad and short ; bursa copulatrix projecting ; vagina short, without tubular sclerotised part.

Spermatheca (fig. 130) with capsule smooth and uniformly sclerotised ; collum not differentiated ; ramus projecting as an antero-lateral chamber, rounded apically ; spermathecal duct short, leaving capsule through an invaginated tube and entering bursa copulatrix on ventral right-hand side ; gland ovoid, and entering ramus through an invaginated funnel.

Rhynchaenus fagi (L.) (fig. 131)

Ovarioles with terminal filaments and ligaments ; lateral oviducts not of uniform diameter, without distinct calyx ; common oviduct short and broad ; bursa copulatrix absent ; vagina narrow anteriorly, broad posteriorly, without tubular sclerotised tube.

Spermatheca (fig. 132) with capsule not uniformly sclerotised, smooth and broad anterior end, narrow, blunt apex ; collum tubular, curved, with base invaginated ; ramus broad, rounded apically ; spermathecal duct short, continuous with apex of collum, entering dorsal posterior side of common oviduct ; gland almost ovoid with irregular outline, stalked, entering apex of ramus through an invaginated funnel.

Rhynchaenus rusci (Hbst.)

Similar to *R. fagi* but vagina almost rounded on sides ; spermatheca (fig. 133) with capsule very stout ; collum undifferentiated ; spermathecal duct leaving capsule through an invaginated tube ; gland long and tubular.

Rhamphus pulicarius (Hbst.) (fig. 134)

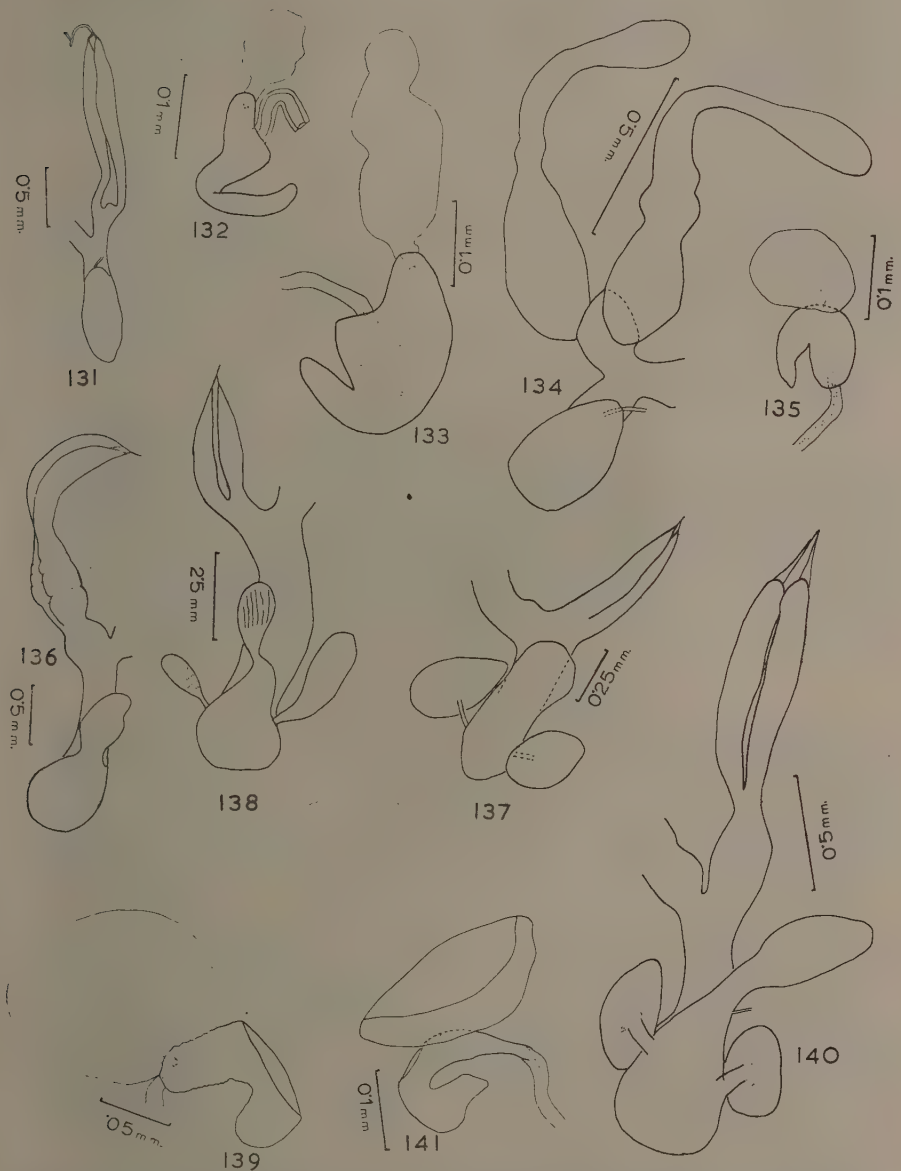
Ovarioles broad and rounded apically, lying freely in the body-cavity, without terminal filaments or ligaments ; lateral oviduct enlarged to form calyx, ovarioles attached to it subapically ; common oviduct broad and short ; bursa copulatrix very small ; vagina short, rounded at sides, without tubular sclerotised posterior part.

Spermatheca (fig. 135) with capsule uniformly sclerotised, comma-shaped ; collum and ramus undifferentiated ; spermathecal duct short, leaving capsule by an invaginated tube and entering junction of bursa and common oviduct ; gland ovoid, entering capsule in the middle externally.

Scolytus destructor Ol. (fig. 136)

Ovarioles short, with terminal filaments but without ligaments ; lateral oviduct forming a small calyx ; common oviduct tubular, longer than lateral oviducts ; bursa copulatrix well developed with a basal neck, closely applied to common oviduct ; vagina short, without sclerotised tubular part.

Spermatheca not seen.



FIGS. 131–141.—(131, 132) *Rhynchaenus fagi*: (131) female reproductive organs; (132) spermatheca. (133) Spermatheca of *R. rusci*. (134–135) *Rhamphus pulicarius*: (134) female reproductive organs; (135) spermatheca. (136–137) Female reproductive organs of: (136) *Scolytus destructor*; (137) *Hylastinus obscurus*. (138, 139) *Phloeophthorus rhododactylus*: (138) female reproductive organs; (139) spermatheca. (140, 141) *Myelophilus piniperda*: (140) female reproductive organs; (141) spermatheca.

Hylastinus obscurus (Marsh.) (fig. 137)

Ovarioles with terminal filaments and ligaments; lateral oviducts short, broad, without distinct calyx; common oviduct tubular, longer than lateral oviducts; bursa copulatrix well developed, longer than vagina; vagina short, without sclerotised tubular part; one conical symbiont-containing structure entering each side of vagina through a tube attached at about middle of structure.

Spermatheca not seen.

Phloeophthorus rhododactylus (Marsh.) (fig. 138)

Ovarioles short with terminal filaments but without ligaments; lateral oviducts narrow and short, common oviduct longer, much broader than lateral oviduct; bursa copulatrix well developed, with a long narrow stalk carrying a club-shaped sclerotised apex; vagina short, without sclerotised tubular part; one club-shaped symbiont-containing structure entering vagina on each side through a narrow tube.

Spermatheca (fig. 139) with capsule having a hollow pit external to bend, both arms of almost equal diameter and sclerotised, anterior one reticulate; collum and ramus undifferentiated; spermathecal duct short (entry into the system not seen); gland ovoid, entering capsule through an invaginated funnel inferior to entry of duct.

Myelophilus piniperda (L.) (fig. 140)

Ovarioles short, with terminal filaments but without ligaments; lateral oviducts broadened to form small calyx; common oviduct narrower than lateral oviducts; bursa copulatrix well developed, constricted and then broadened apically; vagina short, without tubular sclerotised part; one symbiont-containing structure entering vagina on each side.

Spermatheca (fig. 141) with capsule of characteristic shape, reticulate; with hollow external depression posterior to entry of gland; collum projecting, narrowed apically; ramus undifferentiated; spermathecal duct short (entry into the system not seen); gland ovoid, vesiculate (shrunk in the figure), entering capsule externally through a funnel-shaped invagination.

V. The Male Reproductive System

The male reproductive organs in the Curculionidae *s.l.* consist of a pair of testes, vasa efferentia and vasa deferentia, the ejaculatory duct, one or more pairs of accessory glands and the vesiculae seminales (sometimes absent). The testes are creamy or white in colour and lie one on each side of the alimentary canal in all species studied except *Balanobius pyrrhoceras*, where they are medially apposed and lie above the alimentary canal, enclosed in a common sheath but giving rise to two independent vasa deferentia.

Each testis is single or bilobed; it may comprise one or more follicles. The bilobed testis either has the lobes free or enclosed in a common sheath. The free lobes are spherical, while the enclosed ones are broadly oblong but constricted at the point of union of the two lobes. The median side of each lobe gives rise to a vas efferens which is distinct in the free-lobed testes, hardly so in the enclosed testes, and apparently absent in the single-lobed ones. The vas deferens arises directly from the single-lobed testes, whereas the vasa efferentia unite to form it in the bilobed ones. The vas deferens varies in length and is usually dilated between its extremities to form the vesicula seminalis, which therefore divides the vas deferens into an anterior and a posterior part. The vesicula seminalis is either opaque and small or transparent and large. The latter type may be lobed or spherical and unlobed.

The accessory glands are usually present; they may be simple or bifurcate and two in number, or there may be two or more pairs of simple glands. In the bifurcate gland one branch is usually longer than the other. The glands are tubular, vary in length, are coiled or simple and are narrow, elongate-ovoid or almost spherical in shape, and they join the anterior side of the vesicula seminalis along with the vas deferens. The vas deferens from each testis unites with its fellow of the opposite side to form the ejaculatory duct which varies in length and diameter.

Short descriptions of the male reproductive system of various species are given in the following pages.

Rhynchites pauxillus Germ. (Rozsypal, 1939)

Testes, two, free-lobed; vasa efferentia distinct, free from testis; anterior part of vas deferens longer than posterior one; vesicula seminalis large and unlobed; three tubular accessory glands present.

Apion miniatum Germ. (fig. 142)

Each testis bilobed, lobes enclosed in a common sheath; each lobe almost spherical (different in shape in mature adults), with one follicle, one lobe smaller than the other, vasa efferentia not visible; vasa deferentia swollen anterior to entrance of gland, posterior part narrow; vesicula seminalis absent; one two-branched accessory gland entering each vas deferens before middle, one branch long, tubular and coiled, the other short and ovoid, ejaculatory duct narrowed posteriorly.

Apion ulicis (Forst.)

Similar to *A. miniatum* except that the lobes of each testis are almost of equal size and only one accessory gland is present.

Davies (1928) has, incorrectly, shown vasa efferentia (his paired vasa deferentia) arising independently from each lobe. He mentioned the anterior swollen part of the vas deferens as the probable vesicula seminalis, as did also Phelps (1956) in *Piezotrachelus varius* and *Apion chirindanum*. I do not, however, agree with these authors. The vesicula seminalis in all Rhynchophora studied by me and by others is the swollen part of the vas deferens into which the accessory glands, whether paired or unpaired, open anteriorly. In some curculionids, however, the swollen vas deferens is present as well as the true vesicula seminalis.

Apion frumentarium (Payk.)

Similar to *A. miniatum* except that the lobes of the testis are of equal size.

Apion immune Kirby

Similar to *A. miniatum* except that the branches of the accessory gland are tubular, one shorter than the other and the ejaculatory duct is of uniform diameter.

Myllocerus sp. nov. (fig. 143)

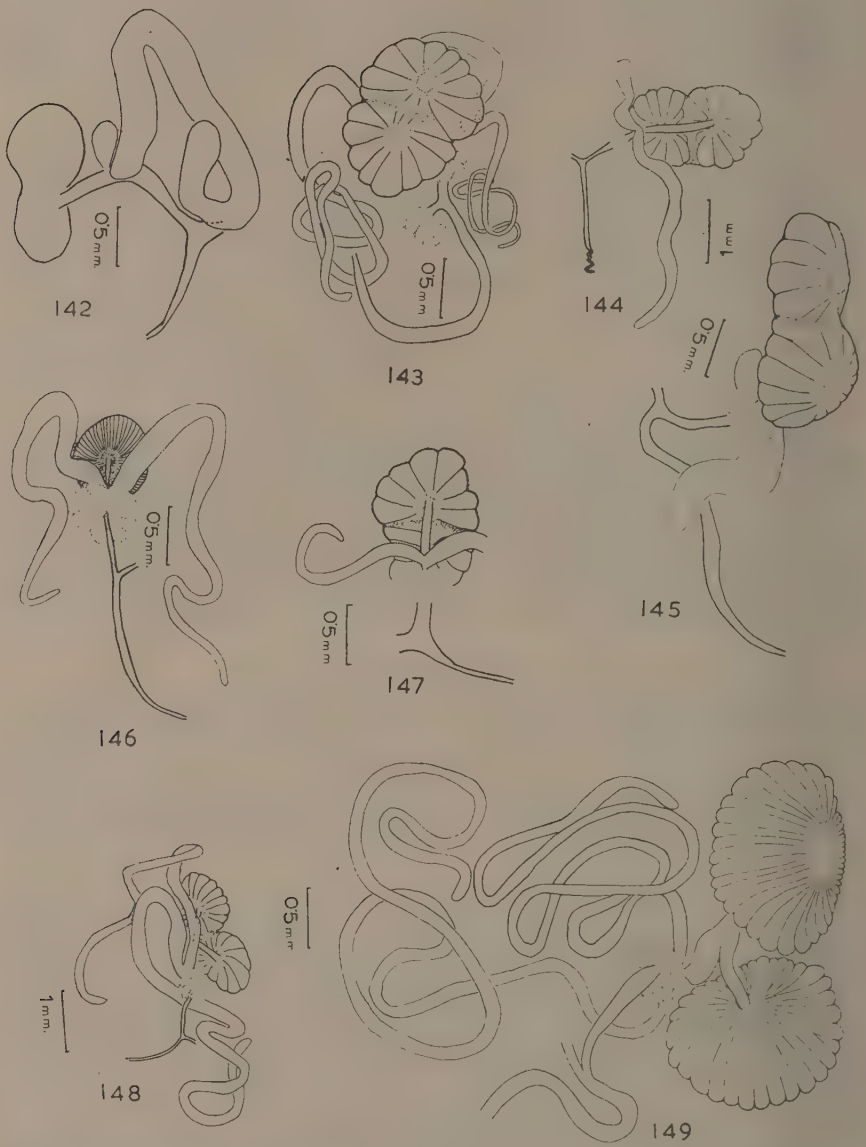
Each testis large, bilobed, lobes enclosed in a common sheath, pressed together and broadly ovoid; each lobe with 8–10 distinct follicles and further indistinct ones near junction of the two lobes; vasa efferentia closely applied to lobes and uniting close to testis to form vas deferens; vasa deferentia short: vesicula seminalis large, transparent, eight-lobed, situated on anterior half of vas deferens; one two-branched gland on each side, each branch very long, coiled, tubular and joined to its fellow branch just before entering vesicula seminalis; ejaculatory duct long, broadest at about middle, narrowing in front and behind.

Myllocerus maculosus Desb.

Agrees in general with the above species except that one lobe of the testis is narrower than the other and without a constriction at the point of union; there are more than seven follicles distinct in each lobe.

Phyllobius pyri (L.) (fig. 144)

Each testis bilobed; lobes enclosed in a common sheath, pressed together and oblong, with a constriction at point of union; each lobe with 12–14 follicles; vasa efferentia distinct and short; vas deferens long, broader on anterior side of vesicula seminalis than on its posterior side;



Figs. 142–149.—Male reproductive organs of: (142) *Apion miniatum*; (143) *Mylloceras* sp. nov.; (144) *Phyllobius pyri*; (145) *Parisomias* sp. nov.; (146) *Amblyrrhinus subrecticollis*; (147) *Sitona regensteinensis*; (148) *Hypolixus truncatulus*; (149) *Conorhynchus brevirostris*.

vesicula seminalis large, transparent, eight-lobed, situated on vas deferens behind middle ; one two-branched gland entering vas deferens a little distance before vesicula seminalis ; each branch long, tubular, joining the other just before entering vas deferens, one branch shorter and thicker than the other ; ejaculatory duct long, coiled, tapering posteriorly.

Phyllobius virideaeris (Laich.)

Similar to *P. pyri* except that each testis is oblong without constriction, and each lobe has 7–8 follicles.

Polydrosus tereticollis (DeGeer)

Each testis irregularly shaped, bilobed, enclosed in a common sheath ; follicles not distinct (adults immature) ; vasa efferentia indistinct ; vas deferens clearly defined on both sides of vesicula seminalis ; vesicula seminalis large, transparent, eight-lobed, lying at about middle of vas deferens ; one two-branched accessory gland, tubular, one branch narrower and shorter than the other, entering vesicula seminalis on its anterior side ; ejaculatory duct long and narrowed posteriorly.

Parisomias sp. nov. (fig. 145)

Each testis large, bilobed, lobes enclosed in a common sheath ; each lobe subspherical, with 13–14 follicles ; vasa efferentia short, applied to the lobes, indistinct ; vas deferens shorter on anterior of vesicula seminalis than on its posterior ; vesicula seminalis large, transparent, with 6–9 unequal lobes, situated close to testis ; one short, thick accessory gland entering each vesicula seminalis through a tube on anterior side.

In one specimen I noted a three-lobed testis on one side and a two-lobed one on the other.

Amblyrrhinus subrecticollis Marsh. (fig. 146)

Each testis small and bilobed, lobes enclosed in a common sheath, with a large number of small follicles in the specimens studied ; vasa efferentia not visible ; vas deferens visible on both sides of vesicula seminalis, longer on its posterior side than anterior part ; vesicula seminalis large, transparent and eight-lobed ; one two-branched accessory gland joining vas deferens just before vesicula seminalis, each branch long, tubular, coiled and uniting with its fellow branch before entering the system ; ejaculatory duct broader in middle and narrowed to both extremities, more so posteriorly.

Amblyrrhinus sp. nov.

Similar to *A. subrecticollis*.

Sitona regensteinensis (Hbst.) (fig. 147)

Each testis bilobed and oblong, lobes enclosed in a common sheath ; each lobe with 8–9 follicles ; vasa efferentia short and distinct ; anterior part of vas deferens narrower and longer than posterior part ; vesicula seminalis large, transparent, eight-lobed ; one two-branched, tubular, coiled accessory gland on each side, one branch longer than the other, joining it before entering vesicula seminalis ; ejaculatory duct broad at point of union of vasa deferentia, then tapering posteriorly.

Sitona sp.

Similar to *S. regensteinensis* except that each lobe of the testis has 13–14 follicles and the ejaculatory duct is not so much broader at the junction of the vasa deferentia but narrower posteriorly.

Hypolixus truncatulus Fab. (fig. 148)

Each testis small, bilobed, lobes free ; each lobe spherical, with numerous follicles ; vasa efferentia arising distinctly from each lobe and uniting free from the lobes to form the vas deferens ; vas deferens thick on anterior side of vesicula seminalis, very narrow posterior to it ; vesicula seminalis large, transparent, with many variably sized lobes ; one two-branched accessory gland entering vesicula seminalis on its anterior side, each branch long, coiled and tubular ; ejaculatory duct short, narrowing posteriorly.

In one male the lobes of the testis were enclosed in a common sheath and just touching one another.

Conorhynchus brevirostris Gyll. (fig. 149)

Each testis bilobed, lobes free ; each lobe spherical, with numerous follicles ; vasa efferentia distinct and free from lobes ; anterior part of vas deferens shorter and thicker than posterior one ; vesicula seminalis large, transparent, made up of a large number of small lobes ; one two-branched accessory gland entering vesicula seminalis on anterior side, each branch long, tubular and coiled ; ejaculatory duct short, narrowed posteriorly.

Xanthochelus faunus Ol.

Similar to *Conorhynchus*, except that the anterior part of the vas deferens is narrower than the posterior one.

Chararas (1956) has studied the male reproductive system in *Rhyncolus porcatus*, *R. elongatus*, *Pentarthrum huttoni* and *Caulotrupis aeneopiceus*. He has indicated three accessory glands in the first species and two in the others on each side, but emphasises the extreme diversity in the male genital organs in groups and species. Testes, in cossonids, are single-lobed.

Bagous sp. (fig. 150)

Each testis oblong and bilobed, lobes enclosed in a common sheath ; each lobe with 7–8 follicles ; vasa efferentia arising free from each lobe ; vas deferens divided into two parts by vesicula seminalis, anterior part longer and narrower than posterior one ; vesicula seminalis large, transparent, six-lobed, lobes of variable size ; one two-branched accessory gland entering vesicula seminalis on its anterior side, one branch shorter and thicker than the other but both branches long, tubular and coiled ; ejaculatory duct short, narrowed posteriorly.

Dorytomus tortrix (L.) (fig. 151)

Each testis bilobed, lobes enclosed in a common sheath, varying in outline, each lobe with follicles distinct externally but indistinct at union of lobes ; vasa efferentia running along each lobe, not free ; vas deferens divided by vesicula seminalis into two almost equal parts, anterior part narrower than posterior one ; vesicula seminalis transparent, eight-lobed ; accessory glands absent ; ejaculatory duct short, gradually narrowed posteriorly.

Dorytomus rufatus (Bed.)

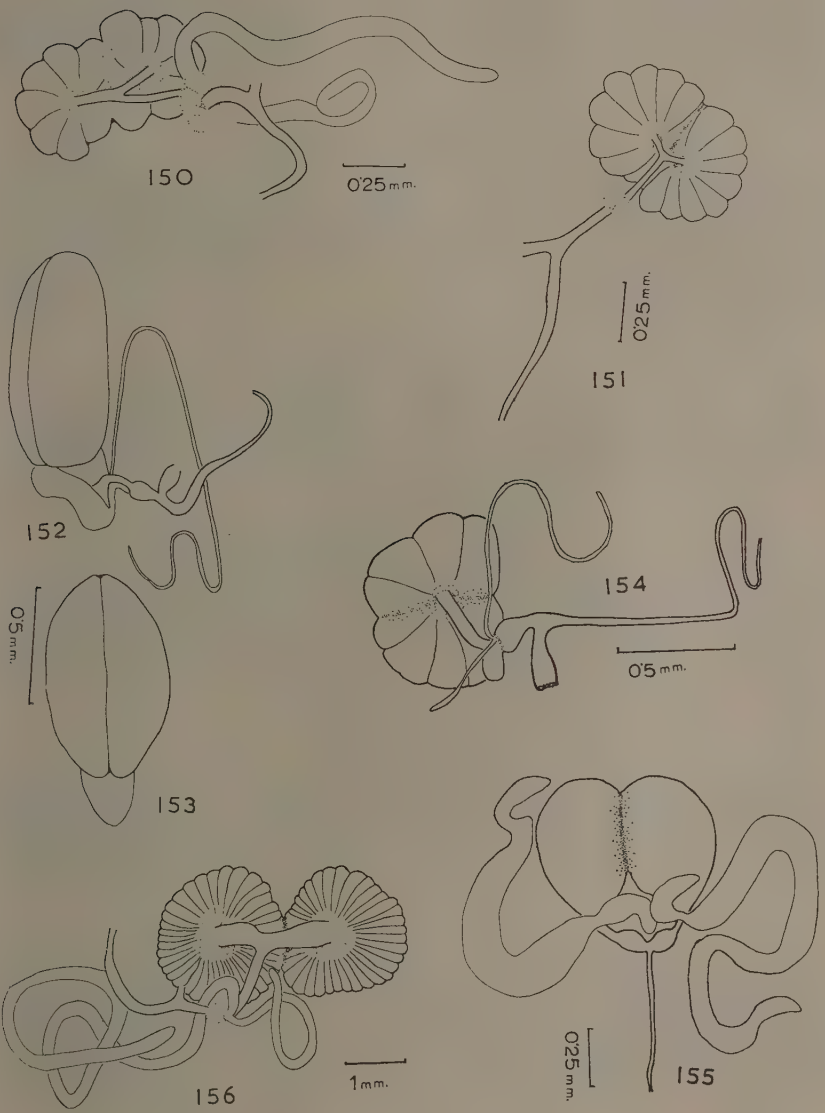
Similar to *D. tortrix* except that each lobe has 5–7 follicles and the ejaculatory duct is short, thick in the middle and tapering to both ends.

Dorytomus dejeani (Fst.)

Similar to *D. tortrix*.

Miccotrogus picirostris (Fab.) (figs. 152 and 153)

Each testis ovoid, single lobed ; follicles arranged transversely in two apposed rows ; vasa efferentia not visible ; vas deferens swollen at base, then continued as a narrow tube before enlarging near apex to form vesicula seminalis ; vesicula seminalis opaque, unlobed ; two accessory glands entering vesicula seminalis on its anterior side, one short, broad and narrowing before its entry, the other coiled, very long and very narrow ; ejaculatory duct short, tapering posteriorly.



FIGS. 150–156.—Male reproductive organs of: (150) *Bagous* sp.; (151) *Dorytomus tortrix*; (152, 153) *Miccotrogus picirostris*; (154) *Anthonomus pedicularius*; (155) *Balanobius pyrrhoceras*; (156) *Hylobius abietis*.

Sibinia arenariae Steph.

Each testis single-lobed, spherical or ovoid, with several follicles (number not clear in the specimens dissected); vasa efferentia not visible; vas deferens short, that part of it anterior to vesicula seminalis longer than posterior part, vesiculae seminales very close to each other at junction of vasa deferentia, spherical, unlobed and transparent; one short, tubular accessory gland bending round vas deferens and entering vesicula seminalis by means of a short duct from middle of gland, which thus may be mistaken for two-branched; ejaculatory duct long; narrow anteriorly to middle, then broader posteriorly.

Anthonomus pedicularius (L.) (fig. 154)

Each testis bilobed, lobes enclosed in a common sheath; each lobe ovoid, with 4–5 follicles, vasa efferentia not visible; vas deferens with anterior part longer than posterior one, latter thicker and enlarged to form the unlobed vesicula seminalis; vesicula seminalis with small transparent bead-like structures all round its anterior margin; two accessory glands on each vas deferens, one with two unequal, narrow tubular branches, the other thick and short; ejaculatory duct long, coiled, narrowed posteriorly.

Anthonomus pomorum (Miles, 1923) is similar to *A. pedicularius*.

Anthonomus inversus Bed.

Similar to *A. pedicularius* except that the vesicula seminalis is without transparent bead-like structures anteriorly, only one two-branched accessory gland is present and the ejaculatory duct is of uniform thickness.

Balaninus glandium (Marsh.)

Each testis bilobed, lobes enclosed in a common sheath; each lobe spherical, touching the other without pressing against it, with numerous follicles; vasa efferentia very short, not visible between lobes of testis; vas deferens long, part anterior to vesicula seminalis shorter than posterior part; vesicula seminalis small, unlobed; one two-branched accessory gland, both branches long, coiled and tubular, as thick as posterior part of vas deferens, entering it just before its entry into vesicula seminalis; ejaculatory duct long and narrowed posteriorly.

Curculio caryae Horn

Bissel (1937) has shown a bilobed testis on each side, each lobe with 20 follicles, and free from each other; vasa efferentia free from lobes, vesicula seminalis small and unlobed and two tubular accessory glands entering vesicula seminalis on anterior side.

Balanobius pyrrhoceras Marsh. (fig. 155)

Both testes medially apposed, enclosed on a common sheath and lying above alimentary canal; each testis single-lobed and without distinct follicles; vasa efferentia absent; vas deferens short, enlarged posteriorly to form vesicula seminalis; vesicula seminalis not lobed; single, tubular, bifurcate accessory gland on each side, one branch much longer than the other, entering vas deferens just before vesicula seminalis; ejaculatory duct gradually narrowed posteriorly.

Balanobius salicivorus (Payk.)

Similar to *B. pyrrhoceras* except that each testis has 4–7 follicles and the vas deferens is a little longer posterior to vesicula seminalis.

Hylobius abietis (L.) (fig. 156)

Each testis bilobed, lobes free; each lobe spherical, with numerous follicles; vasa efferentia free from lobes, broader anteriorly; vas deferens narrower than vas efferens, its anterior part longer than posterior one; vesicula seminalis large, transparent, many-lobed; one long, tubular,

coiled accessory gland entering vesicula seminalis through a narrow tube nearer to one end of the gland, which thus appears two-branched ; ejaculatory duct gradually tapering posteriorly.

Munro (1914) and Nüsslin (1911, 1913) have also studied this species.

Pissodes (Hopkins, 1911) has two free spherical lobes in each testis, the vasa efferentia distinct and free from the lobes of the testis : and the vesicula seminalis unlobed and spherical with two accessory glands on each side.

Hypera murina (Fab.) (fig. 157)

Each testis bilobed, lobes enclosed in a common sheath ; each lobe almost spherical and with 9–12 follicles ; vasa efferentia free from lobes, though very close to them ; vas deferens thin, with anterior part longer than posterior one ; vesicula seminalis transparent, eight-lobed ; two accessory glands, one long, tubular, coiled and entering vesicula seminalis by a duct between its ends, thus appearing two-branched, second gland short, ovoid and very close to vesicula seminalis ; ejaculatory duct long, broadest in middle, tapering to both extremities, more so posteriorly.

Hypera punctata (Fab.)

Similar to *H. murina* except that each lobe of the testis has numerous follicles ; the vesicula seminalis has more than eight lobes and the tubular gland is clearly two-branched.

Gronops lunatus F. (fig. 158)

Each testis single-lobed, almost spherical and with seven follicles ; vasa efferentia not visible ; vas deferens with anterior part allied to the testis but longer and broader than the posterior part ; vesicula seminalis transparent and eight-lobed ; one short, tubular accessory gland broader at one end and entering the vesicula seminalis by a duct given off between its extremities, which gives it a two-branched appearance.

Sitophilus granarius (L.)

Müller (1928) has shown one bilobed testis on each side, lobes enclosed in a common sheath ; vasa efferentia not visible, vas deferens with anterior part longer than the posterior one ; vesicula seminalis lobed and transparent with one accessory gland and the ejaculatory duct tapering posteriorly.

Andersen (1936) and Krautwig (1930) have also studied this species.

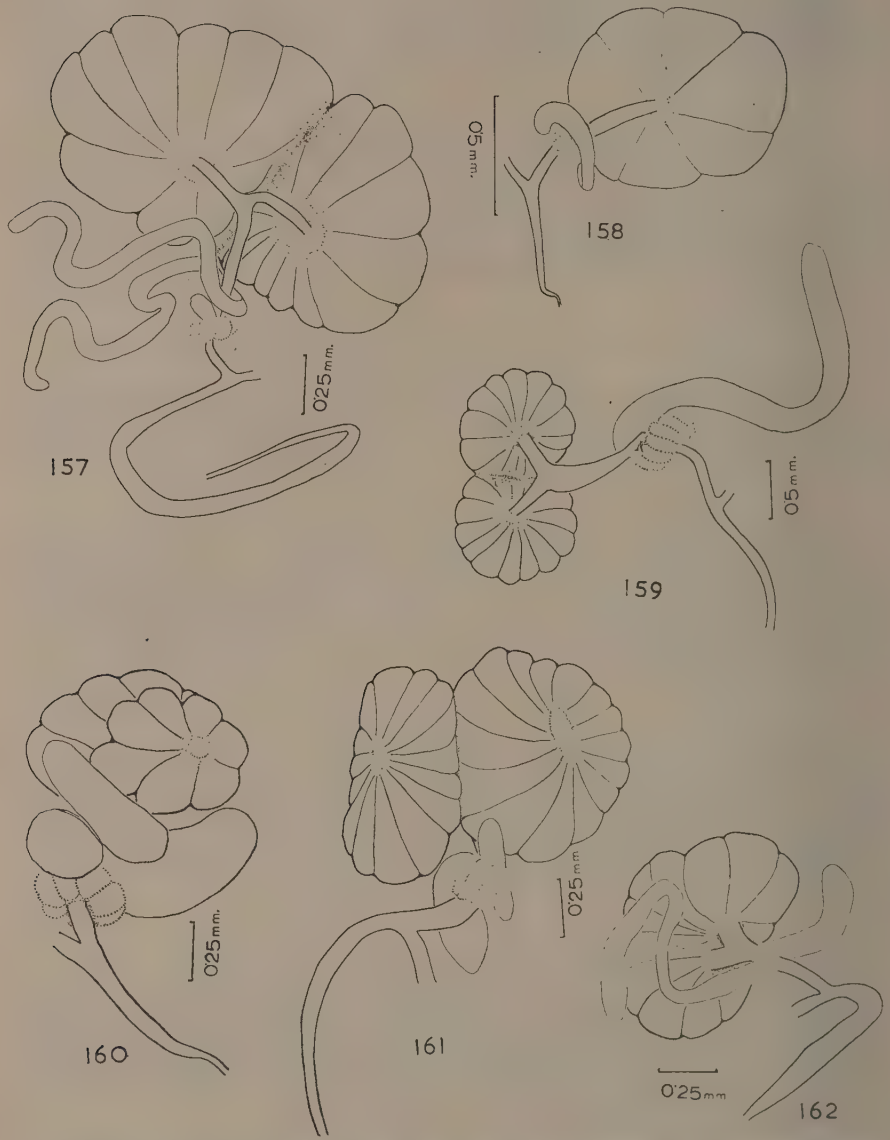
S. oryzae has been studied by Murray and Tiegs (1935).

Cosmopolites sordidus Aur. (fig. 159)

Each testis bilobed, lobes free in some specimens, in others enclosed in a common sheath and jointly constricted at their union ; each lobe almost spherical, with 12-15 follicles ; vasa efferentia free from lobes ; vas deferens with anterior part narrowing to vesicula seminalis, longer than posterior narrow part ; vesicula seminalis transparent, large, with many lobes of variable size ; one tubular accessory gland entering each vesicula seminalis anteriorly ; ejaculatory duct short and of almost uniform diameter.

Rhynchophorus sp.

Each testis bilobed, lobes free ; each lobe spherical, with numerous follicles ; vasa efferentia free from lobes, narrower than vas deferens ; vas deferens coiled, its anterior part very much longer than posterior part ; vesicula seminalis transparent, many-lobed ; single tubular accessory gland very long and coiled, entering each vesicula seminalis anteriorly ; ejaculatory duct coiled and of almost uniform diameter.



Figs. 157–162.—Male reproductive organs of: (157) *Hypera murina*; (158) *Gronops lunatus*; (159) *Cosmopolites sordidus*; (160) *Cidnorrhinus quadrimaculatus*; (161) *Ceuthorrhynchus pollinarius*; (162) *Rhinoncus pericarpius*.

Coeliodes rubicundus (Hbst.)

Each testis bilobed, lobes lying at acute angle to each other, enclosed in a common sheath ; each lobe spherical externally, with 6–10 follicles ; vasa efferentia not visible ; vas deferens short ; vesicula seminalis transparent, eight-lobed, at about middle of vas deferens ; two accessory glands entering each vesicula seminalis anteriorly ; one long and tubular, the other short and thick ; ejaculatory duct short, thicker than vas deferens.

Micrelus ericae (Gyll.)

Each testis bilobed, lobes small, enclosed in a common sheath, follicles not distinct ; vasa efferentia not visible ; vas deferens enlarged, close to testis (thus appearing like a testicular lobe), narrowed to vesicula seminalis ; vesicula seminalis transparent, indistinctly lobed ; two broad accessory glands entering each vesicula seminalis anteriorly through narrow tubes running side by side, one gland longer and broader than the other ; ejaculatory duct short and stout.

Stenocarus fuliginosus Marsh. (Rozsypal, 1941) is similar to *Micrelus ericae*.

Cidnorrhinus quadrimaculatus (L.) (fig. 160)

Each testis bilobed, lobes facing each other and enclosed in a common sheath ; each lobe almost spherical, with 5–7 follicles ; vasa efferentia not visible ; vas deferens very short ; vesicula seminalis transparent, eight-lobed ; two accessory glands, the short one a simple tube, the other, larger one entering vesicula seminalis by a duct from between its ends, thus appearing two-branched ; ejaculatory duct tapering to apex.

Ceuthorrhynchus pollinarius Forst. (fig. 161)

Each testis bilobed, lobes at acute angle to each other and enclosed in a common sheath ; each lobe of variable shape, with 14–16 follicles ; vasa efferentia not visible ; vas deferens very short ; vesicula seminalis transparent, eight-lobed ; two short accessory glands entering vesicula seminalis on anterior side, the thinner, short one being two-branched ; ejaculatory duct gradually tapering to posterior end.

Rhinoncus pericarpius (L.) (fig. 162)

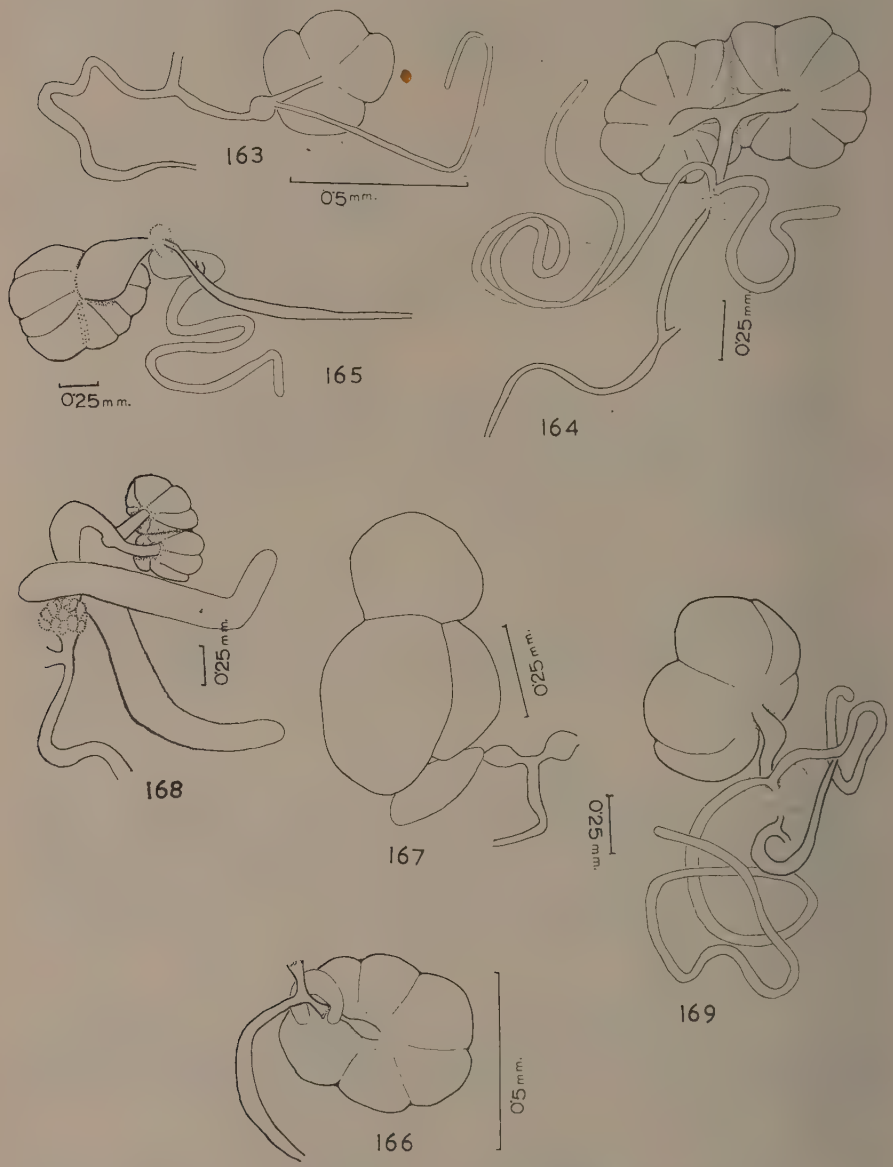
Each testis bilobed, lobes almost at right angle and enclosed in a common sheath ; each lobe of variable shape (usually almost spherical), with 10–12 follicles ; vasa efferentia not visible ; vas deferens with broad anterior part and narrow posterior part ; vesicula seminalis transparent and five- to eight-lobed ; one two-branched accessory gland entering vesicula seminalis anteriorly, one branch long, coiled and gradually broadened to apex, the other shorter and broader ; ejaculatory duct short, broad in middle and narrowed to both ends.

Gymnetron pascuorum (Gyll.) (fig. 163)

Each testis single-lobed, almost spherical, with 3–5 follicles ; vasa efferentia absent ; vas deferens long, anterior part shorter than posterior ; vesicula seminalis unlobed and opaque, one long, narrow, tubular, coiled accessory gland entering vesicula seminalis on anterior side ; ejaculatory duct long, coiled, broader at about middle and tapering to both ends.

Alcidodes fabricii Fab. (fig. 164)

Each testis small, bilobed, lobes enclosed in a common sheath ; each lobe almost spherical and with 9–11 follicles ; vasa efferentia broad, free from lobes, but close to them ; vas deferens long, distinct on both sides of vesicula seminalis, with anterior part broader than posterior one ; vesicula seminalis transparent, eight-lobed ; one tubular accessory gland entering vesicula seminalis on anterior side, composed of two unequally long branches ; ejaculatory duct long, slightly narrowed posteriorly.



Figs. 163–169.—Male reproductive organs of: (163) *Gymnetron pascuorum*; (164) *Alcidodes fabricii*; (165) *Cionus scrophulariae*; (166) *Rhynchaenus fagi*; (167) *Rhamphus pulicarius*; (168) *Scolytus destructor*; (169) *Hylastinus obscurus*.

Cionus scrophulariae (L.) (fig. 165)

Each testis bilobed, lobes lying at an angle to one another ; each lobe almost spherical, with 7–12 follicles of unequal size ; vasa efferentia not visible ; anterior part of vas deferens swollen and narrowed to vesicula seminalis, posterior part tubular ; vesicula seminalis transparent, unlobed, bulging to one side opposite the entry of the gland ; one accessory gland tubular, long, coiled, narrow apically but thickened to the base, entering vesicula seminalis on anterior side ; ejaculatory duct broadened in middle, tapering to both ends.

Cionus sp.

Similar to *C. scrophulariae* except that each lobe has 10–13 follicles and the accessory gland is extremely long and coiled.

Rhynchaenus fagi (L.) (fig. 166)

Each testis single-lobed, ovoid, comprising 5–6 follicles ; vasa efferentia absent ; vas deferens swollen close to testis, narrowed to vesicula seminalis, with thick posterior part ; vesicula seminalis opaque, with eight small, transparent bead-like lobes on its anterior margin ; one short, tubular accessory gland entering vesicula seminalis on anterior side, making a semicircle round vas deferens ; ejaculatory duct short, broad in middle, tapering to both ends.

Rhynchaenus rusci (Hbst.)

Similar to *R. fagi* except : anterior part of vas deferens short and not distinct ; vesicula seminalis eight- to ten-lobed, lobes of unequal size ; one short, tubular, two-branched accessory gland with one branch broader and longer than the other ; ejaculatory duct stout, tapering posteriorly.

Rhamphus pulicarius (Hbst.) (fig. 167)

Each testis bilobed, lobes enclosed in a common sheath ; each lobe spherical, comprising a single follicle ; vasa efferentia not visible ; vas deferens swollen, closely attached to testis, broad anteriorly, narrow posterior to vesicula seminalis ; vesicula seminalis large, transparent, unlobed ; one vesiculate accessory gland entering vesicula seminalis anteriorly ; ejaculatory duct short, narrowed posteriorly.

Scolytus destructor Ol. (fig. 168)

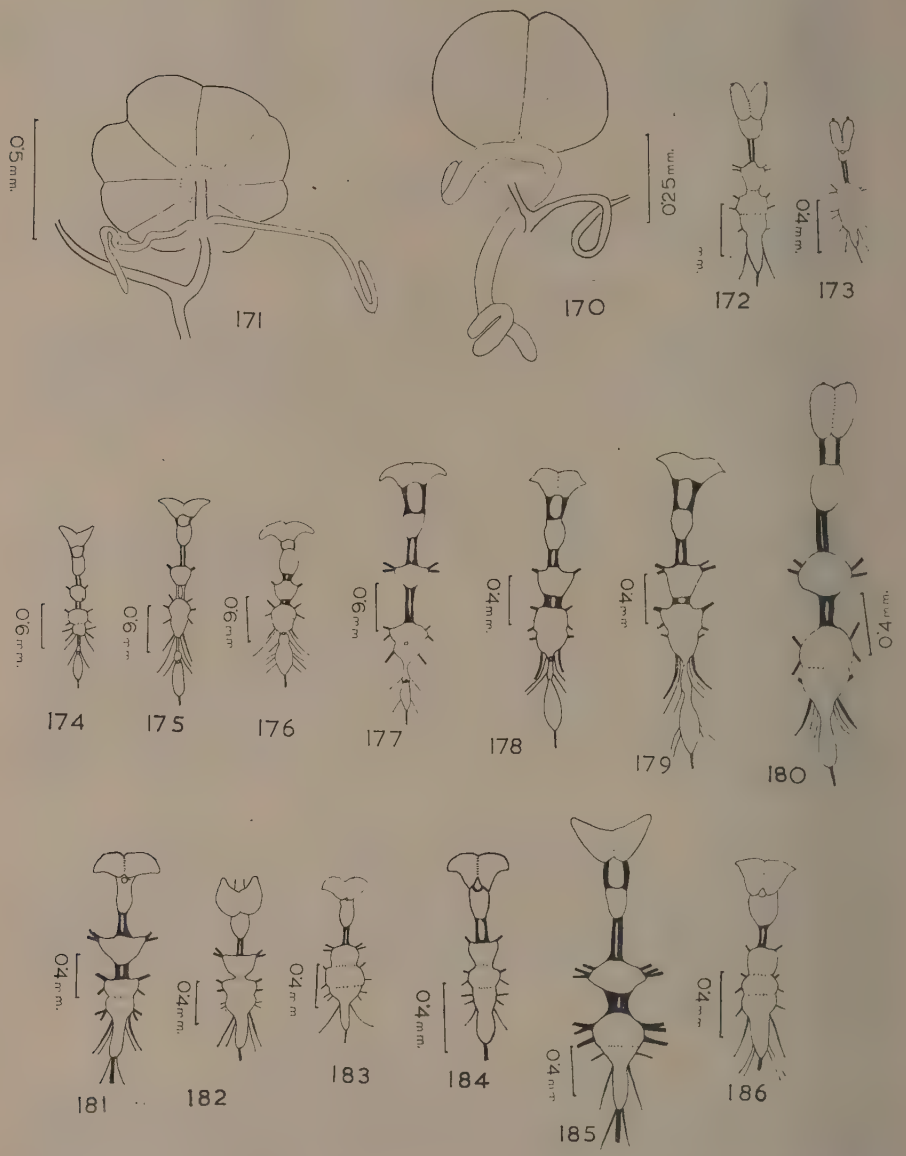
Each testis bilobed, lobes enclosed in a common sheath : each lobe applied to the other in the same plane and not at an angle ; with 5–6 follicles ; vasa efferentia distinct and free from lobes ; vas deferens with anterior part longer and thicker than posterior one ; vesicula seminalis well developed, transparent and many-lobed ; one tubular two-branched accessory gland entering vesicula seminalis anteriorly, both branches of almost equal length and diameter ; ejaculatory duct short, narrow anteriorly.

Hylastinus obscurus (Marsh.) (fig. 169)

Each testis single-lobed, almost spherical, comprising 5–6 follicles ; vasa efferentia absent ; vas deferens with anterior part broader than posterior one ; vesicula seminalis large, transparent, unlobed and spherical ; one tubular, coiled, two-branched accessory gland entering vesicula seminalis anteriorly, one branch longer than the other ; ejaculatory duct short, narrow.

Phloeophthorus rhododactylus (Marsh.) (fig. 170)

Each testis single-lobed, ovoid, with two large follicles ; vasa efferentia not visible ; vas deferens with anterior part swollen and posterior part narrow, tubular ; vesicula seminalis large, transparent, unlobed and spherical ; one accessory gland tubular, coiled, entering vesicula seminalis anteriorly through a narrow tube nearer to one of its extremities ; ejaculatory duct short.



FIGS. 170–186.—(170, 171) Male reproductive organs of: (170) *Phloeophthorus rhododactylus*; (171) *Myelophilus piniperda*. (172–186) Central nervous system of: (172) *Apion miniatum*: (173) *A. ulicis*; (174) *Myllocerus* sp. nov.; (175) *Phyllobius pyri*; (176) *Strophosomus melanogrammus*; (177) *Parisomias* sp. nov.; (178) *Amblyrrhinus subrecticollis*; (179) *Amblyrrhinus* sp. nov.; (180) *Sitona regensteinensis*; (181) *Dorytomus tortrix*; (182) *Anthonomus pedicularius*; (183) *Balanobius pyrrhoceras*; (184) *Coeliodes rubicundus*; (185) *Alcidodes fabricii*; (186) *Rhynchaenus fagi*.

Myelophilus piniperda (L.) (fig. 171)

Each testis single-lobed, spherical or ovoid, with 7–9 follicles ; vasa efferentia not visible ; vas deferens long, divided into two almost equal parts by vesicula seminalis ; vesicula seminalis large, transparent, spherical and unlobed ; one thin, coiled, tubular, two-branched accessory gland entering vesicula seminalis on anterior side, one branch longer than the other ; ejaculatory duct tapering posteriorly.

The male reproductive organs have also been studied in *Phloeotribus scarabaeoides* Bern. (Russo, 1937), *Dendroctonus micans* Klug. (Franke-Grossmann, 1951), *Ips typographus* (L.) (Merker and Wild, 1954 ; Nüsslin, 1913 ; Kühn, 1951) and *I. curvidens* Germ. (Maksymov, 1950).

VI. Discussion and Conclusions

Any discussion of natural relationships within the Curculionidae *s.l.* is handicapped by the limited information available from my work and the previous literature, especially as representatives of some genera of uncertain position could not be studied. An attempt has, nevertheless, been made to assess the value of internal characters at different taxonomic levels, taking each system separately. It may be emphasised that a much larger number of species will have to be studied for the true assessment of their importance in the classification of weevils.

1. *The alimentary canal*

The crop is absent in the Rhynchitinae, Apioninae, Otiorrhynchinae (except Phyllobiini), Sitoninae, Eremninae, Lixini, Erirrhininae, Tychiinae, Anthonominae, Balanininae, Hyperinae, Rhytirrhininae, Ceuthorrhynchinae, Gymnetrinae, Alcidodinae, Anoplinae and Rhynchaeninae. It is well developed in the Attelabinae, Phyllobiini, Brachyderinae, Cleonini, Cossoninae, Bagoinae, Hylobiinae, Rhynchophorinae, Scolytinae and Hylastinae. This character can be used at tribal or subfamily level.

The proventriculus is present in weevils, except for the Rhynchitinae, Attelabinae, Apoderinae, Apioninae, Alcidodinae and some genera like *Lithinus*, *Styanax* and *Platyrhynchus*. In *Apoderus* and *Alcidodes* the blades are represented by rows of bristles internally. Grinding plates have been observed in Rhynchophorinae, Cossoninae, Scolytinae, Hylastinae, *etc.* (Scolytidae) and some genera like *Niphades* and *Niphadonyx*. A trace of plates may be seen in *Myllocerus*, *Parisomias* and Eremninae. The paired or unpaired condition of grinding structures or blades is useful at subfamily, tribal or generic level. The retaining bristles, declivity teeth and brushes of the blade can sometimes be employed taxonomically as low as the specific level.

The presence or absence and arrangement of bristles in the crop or posterior part of the oesophagus is important at levels between the genus and subfamily.

The distended part of the mid gut is usually devoid of enteric caeca except for a few large ones in Cossoninae and numerous small ones in Rhynchophorinae. The tubular part has scattered enteric caeca in Adelognathi, Sitoninae, Cleoninae, Alcidodinae, Balanininae, Hylobiinae, Rhytirrhininae, Rhynchophorinae and Scolytinae but they are arranged in one or two rows or bunches in the others. The latter character is important in grouping or separating subfamilies.

The arrangement of Malpighian tubules is very variable. The usual (primitive) number is six, but there are only four tubules in some Apioninae, some Cossoninae and *Rhamphus*. Two out of the six Malpighian tubules are modified into short symbiont-containing structures in some Apioninae. The six Malpighian tubules are inserted anteriorly in four main ways :

(i) All round the gut in Attelabinae, Hyperinae and Cioninae and separately in *Polydrosus* and *Cryptorrhynchus* on one side only ;

(ii) in a group of three long ones on each side in Rhynchitinae, Sitoninae and Alcidodinae ;

(iii) six long tubules in a group of four on one side and the other two either in a group or separately in Otiorrhynchinae, *Strophosomus*, Hylobiinae, *Baris*, Cleoninae, *Balaninus*, *Rhynchophorus* and *Cosmopolites* ; a group of four enters through a common chamber in *Myllocerus*, *Balaninus*, Cleoninae, *Rhynchophorus* and *Cosmopolites* ;

(iv) two groups, one of four long and one of two short ones, in Apioninae (some), Eremninae, Cossoninae (some), Bagoinae, Erirrhininae, Tychiinae, Anthonominae, *Balanobius*, Rhytirrhininae, Rhynchophorinae (all the six in one chamber), Ceuthorrhynchinae, Gymnetrinae, *Rhynchaenus*, Hylastinae and Scolytinae (four long ones through a common chamber).

Variation in the mode of anterior insertion can be useful in grouping subfamilies or may even be valuable at generic level.

2. *The female reproductive system*

The usual number of ovarioles is two in each ovary, but the Rhynchitinae have more than two, and only one is said to be present in *Rhyncolus porcatus* (Germ.) (Chararas, 1956). This might conceivably be an abnormality, however, as I have noticed three ovarioles on one side and two on the other in *Cidnorrhinus quadrimaculatus* (one specimen only).

A bursa copulatrix is well developed in the Apioninae, Otiorrhynchinae, Brachyderinae (except *Parisomias*), Cleoninae (part), *Dorytomus* (part), *Anthonomus* (part), Balanininae, Ceuthorrhynchinae (part), Anoplinae, *Rhamphus*, Scolytinae and Hylastinae while absent or vestigial in the others. The size of the bursa, however, varies with the age of the adult. This organ is very variable, offering subfamily, generic and specific characters.

The vagina is tubular and sclerotised in the Adelognathi, Balanininae and Ceuthorrhynchinae (part) but as a rule it is short and unsclerotised in all others, including the Sitoninae.

The symbiont-containing structures are either present, one on each side of the vagina (as in Alcidodinae and Hylastinae), or are associated with the membrane between the eighth and ninth sterna, as in Cleoninae. Such structures are present in *Sitona* on the anterior part of the common oviduct.

The spermathecal duct is very long in Otiorrhynchinae, Brachyderinae (part), Eremninae, Sitoninae, Cioninae, but shorter in the others studied. The spermathecal gland is more or less tubular in the Adelognathi, Apioninae (part), Cleoninae (part), Erirrhininae, Anthonominae, Hylobiinae (part), Rhyntirrhininae, *Cosmopolites* and Ceuthorrhynchinae. It is ovoid in others, including the Sitoninae. The structure and shape of the spermatheca and its component parts, and the entry of the duct into the system provide characters at subfamily, tribal, generic and specific level.

3. *The male reproductive system*

The genus *Balanobius* is unusual in having the testes medially apposed above the alimentary canal. In all the others the testes are separate.

Each testis is usually bilobed in the Curculionidae *s.l.* but the Tychiinae, *Balanobius*, Rhytirrhininae, Gymnetrinae and Hylastinae have them single-lobed. The Hylobiinae and Cleoninae possess free-lobed testes, while the others have the lobes enclosed in a common sheath. The vasa efferentia are free from the lobes in the Cleoninae, Bagoinae, Erirrhininae, Hylobiinae, Hyperinae and Scolytinae, somewhat

distinct in Otiorrhynchinae and Sitoninae and indistinct in the others studied or known. These characters appear to be quite constant in subfamilies.

Numerous follicles have been observed in each lobe among the Eremninae, Cleoninae, *Balaninus* and Hylobiinae but most of the Curculionidae have a smaller number of follicles.

The Apioninae are unusual in the absence of a vesicula seminalis ; elsewhere it is usually lobed and transparent (including Scolytinae) but unlobed and transparent in *Sibinia*, Cioninae, *Rhamphus* and Hylastinae and unlobed and opaque in Anthonominae, *Rhynchaenus* and Balanininae. *Anthonomus* and *Rhynchaenus* possess bead-like structures all round the anterior margin.

The male accessory glands are very variable. They may be absent (*Dorytomus*) or one single-branched or two-branched, or two on each vas deferens. Their structure provides characters at subfamily, generic or lower levels.

4. *The central nervous system*

The central nervous system (figs. 172–186) has been studied in only 16 species belonging to 14 genera. The more primitive type of nervous system has been observed in *Myllocerus*, *Phyllobius*, *Strophosomus*, *Parisomias* and *Amblyrrhinus*. In all these the suboesophageal ganglion is separated from the brain by long, well-marked connectives, the prothoracic ganglion is discrete, the meso- and metathoracic ganglia are fused but the abdominal ganglia are represented by two more or less discrete compound ganglia.

The next intermediate group is formed by *Anthonomus*, *Dorytomus*, *Sitona*, *Conorrhynchus* and *Alcidodes*. Here the suboesophageal ganglion is separated by short thick connectives in the first two genera and by long ones in *Sitona*, *Conorhynchus* and *Alcidodes*. The prothoracic ganglion is discrete, while the meso- and metathoracic and the finger-shaped abdominal compound ganglia are all fused together.

The third group includes *Apion*, *Coeliodes*, *Balanobius* and *Rhynchaenus*. In these the suboesophageal ganglion is separated by short thick connectives from the brain, while the three thoracic and the abdominal ganglia are all fused into a compound ganglion

This study suggests that the central nervous system may be of some value in the determination of the relationship of the groups within Curculionidae when seen in a large number of genera, though Hinton (1939) did not consider this to be so in his natural classification of Dryopoidea.

5. *Conclusions*

On the basis of the information now available the following taxonomic conclusions can be drawn.

(*a*) The superfamily Curculionoidea possesses four or six Malpighian tubules, usually cryptonephridic, with very variable anterior insertion and a mid gut with one or more enteric caeca attached to the tubular part. Nüsslin's (1911) contention, that the bursa copulatrix is large in species with an ovipositor, does not hold good.

(*b*) The family Attelabidae has (*i*) no proventriculus, (*ii*) six long Malpighian tubules inserted in a group of three on each side, or all round the mid gut, (*iii*) female reproductive organs with more than two ovarioles in each ovary (a primitive character) and (*iv*) a vagina without posterior tubular part.

(*c*) The family Apionidae of Crowson (1955) and others has (i) four or six Malpighian tubules ; out of six, a group of two are modified into symbiont-containing structures, (ii) no proventriculus, (iii) a mid gut with two rows of enteric caeca on the tubular part, (iv) two ovarioles in each ovary, (v) no marked vesicula seminalis in the male and (vi) a central nervous system of specialised type. It is difficult to

separate this family from Curculionidae on the basis of external characters alone, as stated by Crowson (1955), and it is doubtful whether it should be retained as a family.

(*d*) The family Curculionidae (including Scolytidae) can be defined as usually possessing (i) a proventriculus, (ii) six Malpighian tubules (except *Rhamphus* and some Cossoninae, in which two have apparently been lost), (iii) variably inserted anteriorly and variably applied posteriorly, (iv) females with two ovarioles in each ovary (except that there is only one in each ovary in *Rhyncolus porcatus* as reported by Chararas (1956) and (v) males always with a vesicula seminalis. The presence of six long Malpighian tubules is probably primitive in Curculionidae and two shorter ones or their absence is evidently a secondary reduction as also stated by Stammer (1934).

(*e*) The Curculionidae can easily be divided into the old divisions Adelognathi and Phanerognathi on internal characters. All the Adelognathi have (i) long, tubular and posteriorly sclerotised vagina and (ii) a relatively primitive central nervous system in that they possess discrete suboesophageal and prothoracic ganglia and two more or less defined compound abdominal ganglia. Phanerognathi, on the other hand, possess a short unsclerotised vagina and a progressively specialised central nervous system. The presence of a tubular sclerotised posterior part of vagina in Balaninae and some Ceuthorrhynchinae is evidently an exception to the rule, because these subfamilies are phanerognathous in other respects. It may be mentioned here that the Apionidae are similar to this group and Reitter (1916) also included them as a subfamily under Phanerognathi.

(*f*) According to the division under paragraph (*e*) the Sitoninae should be transferred to Phanerognathi. The characters that support this view are (i) absence of mandibular scar in the adult, (ii) short and not sclerotised vagina, (iii) central nervous system with only one compound abdominal ganglion fused with thoracic ones and (iv) larval spiracle with paired annulated tube. Crowson (1955) referred this genus doubtfully to the Adelognathi.

(*g*) The Rhynchaeninae appear to be related to the Apioninae, as also indicated by Crowson (1955, 1960), on the following basis : (i) proventriculus present or absent in adult, (ii) antenna geniculate or straight, (iii) wing vein *M* above *Cu* absent, *M* + *Cu* making a characteristic curve near the margin (*cf.* Crowson, 1955, fig. 209), (iv) four Malpighian tubules in *Rhamphus*, (v) two-segmented labial palpi, as in *Apion*, (vi) similar central nervous system and (vii) larval abdominal segments with two tergal folds. A study of the genus *Nanophyes* may offer further evidence in this respect.

(*h*) The genus *Alcidodes* is characterised by possessing (i) two tubular symbiont-containing structures on the anterior part of vagina, (ii) long Malpighian tubules inserted anteriorly in a group of three on each side, and (iii) no distinct proventriculus, the blades only represented by rows of bristles as in *Apoderus coryli* (L.) (Nüsslin, 1911). Its true position in the family Curculionidae needs further study.

(*i*) The Tychiinae, Rhytirrhininae and Gymnetrinae agree in having a single-lobed testis on each side, Malpighian tubules inserted in three groups anteriorly and the distended part of the mid gut elongate.

(*j*) The Cleoninae possess (i) four Malpighian tubules inserted in a common chamber and the other two singly on the dorsal and ventral sides, (ii) two symbiont-containing structures entering the membrane between the eighth and ninth sterna and (iii) lobes of testis free from each other with distinct vasa efferentia and numerous follicles. This subfamily resembles Hylobiinae in respect of the testis and vasa efferentia.

(*k*) Grinding plates of the proventriculus are apparently of the same origin and structure in *Sitophilus*, Cossoninae, Scolytinae and Hylastinae. The female reproductive organs are also broadly similar in these subfamilies (as concluded by Chararas (1956)) and the three subfamilies evidently form a very close group.

(*l*) The proventriculus and its grinding plates in the Rhynchophorinae (except *Sitophilus*) are very different in structure and more or less resemble *Peribleptus* Schönh.

(*m*) In addition, the Cossoninae and Rhynchophorinae have enteric caeca on the distended part of the mid gut, large and few in the former but small and numerous in the latter.

(*n*) The proventricular plates in *Niphades* and *Niphadonyx* are similar to those in Cossoninae and Scolytinae, *etc.*

VII. Acknowledgments

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VIII. Summary

1. Detailed descriptions and illustrations of the alimentary canal and reproductive systems of both sexes are given for some 60 species belonging to 44 genera from 25 subfamilies. The central nervous system was also studied in 16 species, representing 14 genera from 12 subfamilies. A general picture of each of these systems is provided for the family as a whole, and the numerous variations on this basic plan are described comparatively. From this information an attempt was made to determine the significance of the various internal characters in the major subdivisions of the family.

2. The superfamily Curculionoidea possess four or six Malpighian tubules, usually cryptonephridic, with variable anterior insertion. The family Attelabidae has more than two ovarioles in each ovary and no distinct proventriculus. The family Apionidae is without proventriculus, has four or six Malpighian tubules and two ovarioles in each ovary, is without vesicula seminalis in the male and has a specialised central nervous system. Its status as a family is doubtful. The family Curculionidae (including Scolytidae) has two ovarioles in each ovary.

3. The adelognath Curculionidae have a long posteriorly sclerotised vagina and a relatively primitive central nervous system, *i.e.* they possess discrete suboesophageal and prothoracic ganglia and two more or less defined compound abdominal ganglia. The phanerognaths, on the other hand, possess a short unsclerotised vagina (except Balanininae and some Ceuthorrhynchinae) and a progressively specialised central nervous system. The subfamily Sitoninae should be transferred to Phanerognathi.

4. The subfamily Rhynchaeninae appears to be related to the Apionidae. The genus *Alcidodes* is characterised by possessing two tubular symbiont-containing structures on the anterior part of the vagina and each blade of the proventriculus is represented by two rows of bristles only. Its true position in the family needs further study. The families Tychiinae, Rhytirrhininae and Gymnetrinae form one group. The Cleoninae possess two symbiont-containing structures entering the membrane of the eighth and ninth sterna, and resemble the Hylobiinae in having free and distinct vasa efferentia and numerous follicles in each testis lobe. The subfamilies Rhynchophorinae, Cossoninae, Scolytinae and Hylastinae possess grinding plates in the proventriculus.

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